S. C. Reed

PROCEEDINGS
OF THE
SEVENTH INTERNATIONAL GENETICAL CONGRESS

EDINBURGH, SCOTLAND

23—30 AUGUST 1939

Edited by

R. C. PUNNETT, M.A., F.R.S.

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THE SEVENTH INTERNATIONAL GENETICAL CONGRESS

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INTRODUCTION

CAREFUL and skilful plans had been made whereby every contribution to these *Proceedings* was to have been finally corrected by its author and checked by the appropriate recorder during the actual congress week. These plans, like so much else, were wrecked and the construction of the *Proceedings* has therefore been a very difficult task. Many members hurried away without having left their manuscripts behind them; it has been impossible to maintain contact with many others, and so there are more titles than papers, and many papers remain uncorrected. However, all these deficiencies will surely be forgiven, for it will be agreed that, in these times especially, the publication of the *Proceedings* of an International Scientific Congress, even though they remain imperfect, is a real service to science and a gesture that can claim a certain magnificence.

NARRATIVE

THE PERMANENT INTERNATIONAL COMMITTEE appointed by the Sixth International Congress of Genetics at Ithaca in 1932 decided to accept the invitation of the Russian geneticists to hold the next congress in the U.S.S.R. in 1937. After the plans for its organization were well advanced, postponement was found to be necessary. As time passed, the International Committee had reason to doubt that the Moscow meeting would take place even in 1938, and began to explore the possibility of holding the congress elsewhere.

The Committee of the Genetical Society of Great Britain, learning that this was so, informed the Chairman of the International Committee that, if and when his Committee was satisfied that the congress could not meet in Moscow in 1938, the Genetical Society of Great Britain would undertake to stage it in Great Britain in 1939. This invitation was ultimately accepted and the Committee of the Genetical Society formed itself into an Organizing Committee. In November 1937 the following note was issued to the Press:

"In accordance with a resolution of the International Committee and with the decision of the Organizing Committee elected by the Genetical Society of Great Britain, the Seventh International Congress of Genetics will meet in Edinburgh in 1939, probably from August 23rd–30th inclusive. Professor F. A. E. CREW, Institute of Animal Genetics, University of Edinburgh, has been appointed General Secretary to the congress and to him all correspondence concerning it should be addressed."

In order to give expression to its view that the British geneticists were acting on the assumption that in this matter they were bringing aid to their colleagues in the U.S.S.R., were building upon the foundations laid by the Russian geneticists, and were expecting these to come in strength to contribute notably to the programme, the Organizing Committee, in February 1938, sent an invitation to N. I. VAVILOV to accept the Presidency of the congress, a position for which, in any case, in virtue of his own eminence, he was the obvious choice.

It was realized from the very beginning that the magnificent and lavish entertainment enjoyed by those who attended the Berlin and Ithaca meetings could not possibly be provided in Great Britain. No financial aid from Government or other sources was to be expected, and consequently the Organizing Committee decided that simplicity and the strictest economy should always be observed.

In April 1938 a first mimeographed circular letter was dispatched to some 3500 biologists likely to be interested, and shortly afterwards the attention of academies, societies and institutions was drawn to the congress and they were invited to be represented thereat by chosen delegates. The British Foreign Office undertook to provide the channel through

which all communications with foreign governments might readily pass, and in many ways began to render great service to the Organizing Committee.

It was quickly decided that the dates originally suggested, 23–30 August, should be those of the meeting. This decision was reached because they were found to be the most convenient for the great majority of the American geneticists. The membership fee was fixed at two guineas. The University of Edinburgh placed at the disposal of the Organizing Committee the five University departments of the King's Buildings group, whilst the committee of the student's King's Buildings Common Room agreed to accept all congress members as honorary members for the duration of the meeting. Six student hostels, conveniently situated and with a total accommodation of 400, were made available. Messrs Pickfords Travel Service were appointed official travel agents and became responsible for the making of all hotel arrangements.

Knowing that a large number of the members, particularly those from America and the continent of Europe, would be travelling to Edinburgh by way of London, a pre-congress tour was arranged and reception committees were formed in London and Cambridge.

As 1938 passed all too quickly, replies came in and a beginning was made with the building of the programme. The following sections began to take shape, and to each of them a Recorder and a Secretary were appointed:

	Recorder	Secretary
A. Gene and Chromosome Theory	H. J. MULLER	D. G. CATCHESIDE
B. Cytology	C. D. DARLINGTON	P. C. KOLLER
C. Physiological Genetics	B. EPHRUSSI	C. H. WADDINGTON
D. Animal Breeding in the light of Genetics	A. D. BUCHANAN SMITH	J. E. NICHOLS (Imperial Bureau of Animal Genetics)
E. Plant Breeding in the light of Genetics	K. MATHER	S. ELLERTON
F. Human Genetics	G. DAHLBERG	L. S. PENROSE and J. A. FRASER ROBERTS
G. Genetics in relation to Evolution and Systematics	J. S. HUXLEY	W. B. TURRILL
H. Statistical Genetics	R. A. FISHER	F. YATES
I. Genetical Aspects of Growth, Normal and Abnormal	C. C. LITTLE	A. W. HADDOW

These officers, together with C. DIVER, R. R. GATES, J. B. S. HALDANE, W. J. C. LAWRENCE, R. C. PUNNETT, E. R. SAUNDERS, A. E. WATKINS, and the GENERAL SECRETARY now became the Organizing Committee. The sectional officers, together with the General Secretary, formed themselves into a subcommittee to deal with matters relating to the programme.

In April 1939 a second mimeographed circular letter was issued to some 1500 geneticists and others who had expressed their interest in the congress affairs. This gave such details as were then available concerning sectional programmes, pre-congress and other tours, and hotel and hostel accommodation in London and Edinburgh.

During June and July of 1939, though every member of the Organizing Committee lost no opportunity for exhibiting an optimism which was certainly unwarranted, it is safe to say that not one of them really thought that the congress would take place. Yet, on the morning of 23 August, the congress membership swiftly passed the 600 mark. But though the congress had met it lacked a President, for on 4 August the following letter had been received:

INSTITUTE OF GENETICS
of the
ACADEMY OF SCIENCES OF THE U.S.S.R.

Bolshaya Kaluzhskaya, 75,
Moscow, U.S.S.R.
26 July 1939.

Professor F. A. E. CREW, *General Secretary,*
Organization Committee of the Seventh
International Congress of Genetics,
Institute of Animal Genetics,
King's Buildings, West Mains Road,
Edinburgh, 9, Scotland.

Dear Professor CREW:

Many scientific institutions of the U.S.S.R., as well as individual Soviet geneticists, received your kind invitation to take part in the Seventh International Congress of Genetics to be held in Edinburgh at the end of August of this year. I also received your kind announcement as to my election by your Organization Committee to the office of President of the Congress.

As you know, the Academy of Sciences of the U.S.S.R. proposed to the International Committee for Genetic Congresses, headed by Professor Mohr (Oslo, Norway), that the Seventh International Congress be held in the U.S.S.R. in 1937. This proposal was accepted by the Committee. Later the Academy of Sciences of the U.S.S.R., with the aim of

making better arrangements for the Congress, proposed that it be postponed until August 1938, to be held, as previously arranged, in Moscow. The International Committee was duly informed of this proposal.

The International Committee, however, postponed the Seventh International Congress of Genetics until 1939 and chose as its place of meeting not the U.S.S.R. but another country. Under such circumstances Soviet geneticists and plant and animal breeders do not consider it possible to take part in the Congress.

I wish to thank the members of your Organization Committee and you personally for the great honour of electing me President of the Congress, and to assure you that I greatly regret the impossibility of participating in the work of the Congress and serving as its President.

Sincerely yours,
(Sgd.) N. VAVILOV.
Director.

This was a blow that stunned. It meant that the programme which had just been printed had to be completely and immediately recast, the titles of 50 papers excised and numerous chairmen replaced. However, the organization, though it was badly strained, did not break down, and the new programme was ready for distribution on 12 August. The presidential chair was left empty, to be filled later when the congress met.

The General Secretary and his staff moved to London to open the congress office there on 15 August. By the end of the following day some 250 members had enrolled. The London Reception Committee (R. A. FISHER, Convenor; Miss B. SCHAFER, Secretary) had arranged the following programme: 15 August. Reception by the Royal Horticultural Society. 16 and 17 August. Visits to Whipsnade Zoological Park; East Malling Research Station; Rothamsted Experimental Station; Royal Horticultural Society Gardens at Wisley; John Innes Horticultural Institution; Courtauld Genetical Laboratory; Natural History Museum, South Kensington; Royal Botanic Gardens, Kew; Zoological Society's Gardens, Regent's Park; Galton Laboratory and Department of Biochemistry, University College; Bureau of Human Heredity; Chelsea Physic Garden.

On 18 August the congress office returned to Edinburgh, and at the same time a party of over 100 left London for Edinburgh by motor coach. They travelled by way of Cambridge where a day and a half were spent. The Cambridge Reception Committee (F. T. BROOKS, Convenor, D. G. CATCHESIDE, Secretary) had arranged the following programme: 18 August, visit to the School of Agriculture and demonstrations by the Plant Breeding Institute, Horticultural Research Station, the Animal Research Station, and in the evening a reception in St John's College. 19 August, visits to the Potato Virus Station, and the Botany School Field Station. In the afternoon a tour of the Colleges and demonstrations in the Botany School by the School of Agriculture, the Botany School, the Strangeways Laboratory and the Zoological Laboratory. 20 August: the party left for Chester via Stratford-on-Avon. On the 21st it halted at Windermere and on the 22nd passed over the Border to reach Edinburgh at 6 p.m., there to be played in by the pipes. That evening there was an enjoyable informal reception by the President and Committee of the Student's Common Room and it seemed that in spite of all our fears the congress was to be amazingly successful.

On the morning of the 23rd the First Plenary Session of the congress took place.

Minutes of the First Plenary Session of the Seventh International Genetical Congress held in the McEwan Hall on Wednesday, 23 August 1939, at 10.30 a.m.

OTTO L. MOHR, Chairman of the Permanent International Committee, was in the Chair.

1. The CHAIRMAN addressed the Congress:

"BAILLIE EDWARD, SIR THOMAS HUDSON BEARE, LADIES and GENTLEMEN,

"At the last International Congress of Genetics at Ithaca a Permanent International Committee was elected and commissioned 'to represent the International Congress until the council of the next congress is formed' and 'to designate the country in which the next congress is to be held'. It was understood that the committee should 'reach its decision concerning the place of the next congress... without special considerations for the countries represented by its chairman or members'.

"At first the possibility of holding the congress in one of the Scandinavian countries was considered. These preliminary discussions led to the result that the Mendelian Society in Lund, Sweden, declared its willingness to arrange the Congress in Lund, Malmö in 1937. Soon afterwards, however, this plan had to be abandoned owing to unforeseen practical difficulties.

"The International Committee then accepted a generous invitation extended by the Presidium of the U.S.S.R. Academy of Sciences to hold the congress in the U.S.S.R. where so much splendid work is being done, both in pure and in applied genetics.

"Preparatory steps for the organization of the Congress in Moscow in 1937 had already been taken when the Soviet committee, quite unexpectedly and without first consulting the International Committee, postponed the congress.

"I am not going to enter here into details regarding the difficulties which lay behind this extraordinary step. The situation was not improved by exaggerated

and utterly incorrect statements which, unluckily, found their way into the foreign press. I shall merely say that, besides practical considerations, very serious differences on fundamental scientific principles were also responsible for the action taken, and the nature of the discussions, also between leading members of the Organizing Committee, was such that the atmosphere seemed anything but propitious for an open, unbiased exchange of scientific opinions.

"The new situation had to be considered by the International Committee. The science of genetics occupies a special position in so far as its principles and practical applications are apt to be interpreted in a political light. This circumstance has during recent years come right to the forefront of public attention. Under these conditions the International Committee found that, all things considered, it would be preferable to hold the congress in a country where this situation was least likely to make itself felt.

"After renewed negotiations the International Committee invited our British friends and colleagues, if possible, to organize the congress in Great Britain, an appeal to which the British geneticists responded in the most generous manner. May I, in the name of the International Committee and, I feel sure, also on behalf of all foreign members, express our deepest gratitude to our British colleagues for the splendid way in which they have been able to overcome all difficulties, difficulties which at times must have seemed almost insurmountable. We are indeed happy and thankful to be here to-day.

"May I also be permitted to convey our respectful and most sincere thanks to the City of Edinburgh and to its ancient University for the hospitality which we are now enjoying.

"Ladies and Gentlemen, the difficulties with which we have been confronted during this inter-congressional period, are, partly at any rate, typical of our time.

"The ultimate achievement of science is the removal of fear. Science has banished the dread of nature's unknown forces, it has checked the devastating, appalling plagues and alleviated human pain to an almost incredible extent. In brief, science has made our earth a far far better dwelling place for man.

"But the *conditio sine qua non* for scientific progress is freedom, freedom of thought, freedom of discussion. If freedom is suppressed, fear, distrust come in again, fear amongst individuals, fear amongst nations. That is where we are to-day, that is why the penetration of a truly international spirit, a scientific spirit in other words, meets so many obstacles just now.

"May this great meeting not only serve to promote our special science, but also to do its share in helping to increase the respect for the basic scientific principles, to the greater welfare of mankind.

"With these words and in this spirit I have the honour to express all our best wishes for the success of the Seventh International Congress of Genetics."

2. The Chairman called upon BAILIE EDWARD, representing the Lord Provost, Magistrates and Councillors of the City of Edinburgh, who conveyed the City's greetings to the Congress.

3. The Chairman, having thanked BAILIE EDWARD, called upon SIR THOMAS HUDSON BEARE, representing the University of Edinburgh, who conveyed the University's greetings to the Congress.

4. The Chairman, having thanked SIR THOMAS HUDSON BEARE, again addressed the meeting:

"In 1938 the Organizing Committee invited VAVILOV to be the President of this congress. I feel sure that I have this assembly with me when I take this opportunity of expressing our appreciation of the readiness and enthusiasm with which our Russian colleagues were willing to undertake the burden of arranging the congress. After the place of the congress had been changed, all through the formative period of the congress, nobody had reason to assume that the Russian geneticists would be unable to attend. Not until ten days before the actual opening of the congress was information received to the effect that none of the U.S.S.R. geneticists would be able to participate. But a body of this size cannot exist without a head. I have taken the opportunity of discussing this matter with the foreign members and everyone I have spoken to gives me support for the suggestion that we, the foreign guests, should by a gesture indicate our admiration for the way in which the British geneticists, under the most difficult circumstances, have served our science by facing the difficulties and overcoming them.

"If it may perhaps appear somewhat irregular for me in my present position to attempt to guide the congress in this manner, I am fully aware that I am no more than expressing the unanimous point of view of the congress members when I suggest that Professor F. A. E. CREW should be invited to be the President of the Congress.

"The volume and spontaneity of the applause permit me to know that this suggestion is unanimously agreed to. I have pleasure and great joy in inviting Professor CREW to accept office."

5. F. A. E. CREW then took the Chair and addressed the congress.

"PROFESSOR MOHR, LADIES and GENTLEMEN:

"To me and to the men of my country the expression of gratitude is easy only when it is the merest formality. When sincerity is involved our emotions

tend to make us mute. And so it is now with me. I am so overwhelmed that my thanks simply will not flow along the channel of words. You are kind: you are too kind. The rewards you give for service are extravagant. It has been easy and it has been pleasant to do those things which I and my colleagues have done in preparation for your welcome here. I should have been far happier had you left me in the relative obscurity of the Secretary's Office, for, speaking biologically, I can say that this is the environment of my own choice. However, even to hesitate in accepting the honour you now pay me would be churlish, and so, as the representative of the geneticists of this country, I now take office.

"I understand that in those places where films are made, every star has his shadow (technically known, I think, as a 'stand-in') who is required to look more or less like his principal and to take his place in the more arduous parts of his role. I would suggest to you that at the moment this is exactly what I am—a stand-in to a star. You invite me to play a part that VAVILOV would have so adorned. Around my unwilling shoulders you drape his robes, and if in them I seem to walk ungainly, you will not forget that this mantle was tailored for a bigger man.

"SIR THOMAS HUDSON BEARE has told you that, twenty and more years ago, thanks to my own promise and prowess I became the first lecturer in genetics in this University. This is not so, for before me there was another—A. D. DARBISHIRE—and the post was created for him. DARBISHIRE died on military service in 1915, and I, living, was later elected to his place. Now, as then, I am a substitute, a second string, and very proud to be such. One thought comforts me. In one respect at least I can claim to be VAVILOV's equal, for I, as he would have done, will serve this congress to the utmost of my ability.

"Ladies and Gentlemen, I am your obedient servant."

6. On a motion from the floor, which was seconded, the following Vice-Presidents were elected:

Vice-Presidents

Argentine:	SAEZ
Australia:	WADHAM
Belgium:	VANDENDRIES
Brazil:	PIZA
Bulgaria:	CHRISTOFF
Canada:	DEAKIN
Chile:	ELGUETA
China:	SHEN
Czecky:	PEKLO
Denmark:	WINGE
Egypt:	KHISHIN
Eire:	DIXON
Estonia:	MADISSOON
Finland:	FEDERLEY
France:	CAULLERY
Germany:	HARTMANN
Gold Coast:	STEWART
Greece:	VLISSIDIS
Hungary:	CSIK
Iceland:	TOMASSON
India:	VENKATRAMAN
Italy:	GINI
Japan:	KOMAI
Jugoslavia:	TAVČAR
Kenya:	ANDERSON
Luxemburg:	SCHNEIDER
Netherlands:	SIRKS
New Zealand:	FRANKEL
Norway:	MOHR
Philippine Islands:	MANRESA
Poland:	MARCHLEWSKI
Portugal:	CAMARA
Roumania:	PARHON
Slovakia:	BABOR
South Africa:	BISSCHOP
Sudan:	TROUGHT
Sweden:	ROSENBERG
Switzerland:	BALTZER
U.S.A.	DEMEREC EMERSON
Uruguay:	BOERGER
Venezuela:	CARVALLO

7. On a motion from the floor, which was seconded, the following were elected members of the Permanent International Committee:

Canada:	HUSKINS
Denmark:	WINGE
France:	EPHRUSSI
Germany:	VON WETTSTEIN
Great Britain:	CREW
Italy:	GHIGI
Netherlands:	SIRKS
Norway:	MOHR
Sweden:	ROSENBERG*
Switzerland:	ERNST
U.S.A.:	DEMEREC

8. On a motion from the floor, which was seconded, the following were elected to the Resolutions Committee:

TIMOFÉEFF-RESSOVSKY	HAGEDOORN
BLAKESLEE	BLARINGHEM
EMERSON	MATHER
FEDERLEY	CREW

9. The Chairman invited Official Representatives to present their credentials at the congress office before 27 August.

10. There being no other business, the congress adjourned until Tuesday, 29 August 1939, at 5 p.m.

For a day and a half the congress was able to immerse itself in its own enjoyable affairs. It even danced. But on the evening of the 24th its serenity was shattered. War, that outmoded futility of irrational immaturity, the antithesis of everything we repre-

* Later, at ROSENBERG's suggestion and on his advice, replaced by DAHLBERG.

sented, was about to overwhelm us. Britishers in Germany had been advised to leave for home. The German delegation, therefore, had no choice but to do likewise; the Poles especially, and with reason, became anxious; whilst the members from the more distant European countries began to worry about transportation difficulties. Indeed, many of the British contingent, sectional officers among them, found it necessary to rush back to anxious families or to leaderless groups. That night and the following day there was an exodus, and Friday found the congress in serious mood. For a time it seemed as though it was doomed to disintegration. But amongst us there were some 150 Americans, Canadians, Australians, New Zealanders, South Africans and others for whom immediate departure was impracticable. These formed a most solid core of immovables, and as long as they remained the congress was in being. The French and Italian delegates, together with many others who acted upon purely personal decisions, exhibited no intention of departing and so encouraged us in our desire to continue. It was thought desirable, however, to advance the second plenary session to Saturday, 26 August, at 6 p.m.

Minutes of the Second Plenary Session of the Seventh International Genetical Congress held in the Zoology Department Lecture Theatre on Saturday, 26 August 1939, at 6 p.m.

1. The Chairman reported that the Permanent International Committee appointed by the congress had met at 9 p.m. on Thursday, 24 August 1939, in the Genetics Department.

Those present were: F. A. E. CREW, M. DEMEREC, B. EPHRUSSI, A. ERNST, A. GHIGI, C. L. HUSKINS, O. L. MOHR, F. VON WETTSTEIN, and Ö. WINGE.

On the motion of O. L. MOHR, F. A. E. CREW was elected Chairman of the International Committee.

It was reported that ROSENBERG found it impossible to accept membership of this committee and that he suggested that DAHLBERG should take his place. It was agreed to announce this suggested change to the congress and ask for its endorsement. This motion was then put to the meeting and the congress unanimously agreed to this alteration in the personnel of the International Committee.

The Chairman then reported that after some discussion the International Committee unanimously agreed that under the circumstances it was quite impossible at this particular time for the International Committee seriously to consider invitations and to decide as to the time and the place of the next congress. It was decided, therefore, that the Committee should report to the congress to this effect and should ask that authority be given to it to designate the time and place of the next congress at some later date.

This motion was put before the Plenary Session, and the congress gave full power to the Permanent International Committee to decide the time and place of the next congress at some later date.

The Chairman further reported that after some discussion the International Committee decided to recommend to the congress that in connexion with future congresses it should not be regarded as essential or even necessary for *Proceedings* to be published. This decision was reached because it was recognized that in the past a number of invitations concerning the place of the congress had not been received from different countries on account of the expensiveness that had been associated with the publication of the *Proceedings*. It was recognized that complete autonomy must be given to the actual Organizing Committee of a particular congress. This committee could publish the *Proceedings* or not, but in order to make it possible for the geneticists of any country to invite a congress to take place in their country, it was decided strongly to make this recommendation to the congress.

This motion was put to the Plenary Session and it was unanimously agreed that the decision whether or not *Proceedings* should be published at future congresses should be left to the Organizing Committee of that particular congress.

The Chairman then called on Professor GHIGI to convey to the congress the invitation from the President of the Istituto Nazionale per le Relazioni Culturali con l'Estero, Roma, for the congress to meet in Rome in 1942, and on Dr BEADLE to convey to the congress the invitation from Stanford University, California, for the congress to be held in California in 1944.

2. The Chairman reported that the Resolutions Committee met in the Genetics Department on Thursday, 24 August, at 9 p.m.

Present: A. F. BLAKESLEE, R. A. EMERSON, and HARRY FEDERLEY.

This meeting considered the resolution put before them by F. A. E. CREW that: "It is desirable that the Congress should set up an International Committee which should devise a scheme or schemes whereby animal and plant stocks of genetical importance might be maintained in times of emergency." The committee decided in favour of the resolution in principle but recognized that it would have to be considered rather carefully in regard to the working out of stock cultures for any single group. The congress unanimously accepted this suggestion.

3. The Chairman then moved that letters of appreciation and thanks should be sent to all those institutions and individuals who had in any way helped towards the success of the congress. The congress unanimously accepted this motion.

The Resolutions Committee, having suggested that a message be sent by the congress to N. I. VAVILOV, the congress instructed the General Secretary to write to him giving him the news of the congress and conveying greetings to all Russian geneticists.

4. A. F. BLAKESLEE moved that "a vote of thanks be extended to the Organizing Committee, to all those who have made the congress a success even under most difficult conditions, and especially to the General Secretary and President who has acted effectively as the leader of the congress".

5. The programme for the rest of the week was discussed and it was decided to shorten the duration of the congress by one day by making Sunday a working day, and that if possible all papers should be read by Monday evening, and that Tuesday should be devoted to exhibits and demonstrations.

6. The Chairman then called upon Mr LAIRD, Secretary of the Department of Agriculture for Scotland, who conveyed to the congress the greetings of the Secretary of State for Scotland and the Minister of Health.

7. The Chairman having thanked Mr LAIRD and there being no other business, the meeting was adjourned *sine die*.

The end of this session found the congress restful again and thereafter everything proceeded almost smoothly, though of course there was much chopping and changing of the remaining parts of the programme. The next three days were enjoyably active, the meetings well attended and the discussions eager and profitable. The only disturbance of any magnitude was when Haldane, presiding at an evening meeting of the "gene group", and at a moment when the atmosphere was still and tense, fell out of his chair with an awe-provoking crash and disappeared behind the lecture bench.

At the farewell party on Tuesday the rebellious rump was most unwilling to depart, and it was not until the early hours of the 30th that it was forced to accept the view that all good things must come to an end. Glasses were filled and we drank to absent friends, those who had shared our bread and wine and who were in danger and distress.

On the morrow news was received that certain sailings had been cancelled and that many others were doubtful; news of profound importance to the Americans. On 1 September fighting began on the German-Polish border, and we knew that it was only a matter of hours before Great Britain would be at war. At a meeting of the American group a committee, consisting of the official delegates appointed by the United States Government, was elected in order to facilitate communication with the American Embassy, the consulate and the travel agents. This committee functioned magnificently, anxiety was quieted and gradually and in small groups the Americans left for home. For some it was indeed a dangerous passage; we knew that some of our colleagues were aboard the *Athenia*, and for many days we remained doubtful as to their fate. We learnt that BRONSON PRICE, COTTERMAN, LAWRENCE and SINGLETON had been saved, but of the TINNEYS we could get no news. If they are dead, as now seems probable, we must remember them; they died in the service of science.

To those Poles who had bravely delayed their departure the road back was now blocked. Whilst awaiting the formation of the Polish Legion in France MARIA SKALIŃSKA found temporary occupation at Kew, and the SLIZYŃSKIS remained at Edinburgh to work.

Had we been left undisturbed, this congress would have been like many another, merely a pleasant affair of no great significance. But the external circumstances which attended it gave it a special quality. We had met as geneticists sharing the same interests and enthusiasms: suddenly we were required to behave as nationals with fiercely conflicting views. We found this demand difficult, irritating, saddening. Our memories of this congress will make us even more fervent servants of peace and of scientific humanism.

OFFICIAL DELEGATES

OFFICIAL DELEGATES NOMINATED BY FOREIGN, DOMINION AND COLONIAL GOVERNMENTS

ALGIERS:
Monsieur le Professeur Caullery.

ARGENTINE:
Engineer Don Mauricio Perez Catan.

AUSTRALIA:
Doctor H.C. Trumble.

BELGIUM:
Monsieur le Professeur de Winiwarter.
Monsieur le Professeur Molhant.
Monsieur Vandendries.

CANADA:
Doctor R.M. Love.
Doctor A. Deakin.

DENMARK:
Professor Øivind Winge.

EIRE:
Mr Richard Lynch.
Mr J.J. Brady.

ESTONIA:
Professor H. Madissoon.

FINLAND:
Professor Harry Federley.

FRANCE:
Monsieur le Docteur Boris Ephrussi.
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Fees from Ordinary Members and Institutional Members	1083	12	0
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Fees from Student Members	14	0	0
Fees partly paid	1	17	8
Contributions to Congress Funds	120	10	7
	£1300	17	3

Expenditure

	£	*s.*	*d.*
Publication of Proceedings	600	0	0
Printing of Programmes	38	1	6
Office Expenses	190	10	2
Secretarial and Clerical Assistance	20	1	3
Laboratory and General Assistance	36	14	6
Exhibits and Demonstrations	71	9	7
Badges	33	17	3
Excursions	9	12	6
Catering, Assistance to stranded members, etc.	37	9	7
Refund of Grant to Genetical Society of Great Britain	100	0	0
Balance:	£	*s.*	*d.*
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	163	0	11
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According to the Programme as it was to have been, the exhibits were to have been arranged and displayed by the exhibitors themselves and accurate descriptions prepared under their personal supervision in time for the official opening of the Exhibit Halls on the second day of the congress. As can now be fully appreciated, these plans never took final shape, and so it was that when the congress ended the materials out of which the Secretary had to build the faithful account of this particular activity, which the Organizing Committee hoped would be found to compare favourably with the truly marvellous exhibits' section of the Ithaca Congress, were found to be very incomplete and inadequate for the purpose. So many and serious were the deficiencies that it was decided that the only course was to give a list (probably itself incomplete) of the contributors.

This is all that can now be done to express the gratitude of the Organizing Committee to those who came so eagerly to its aid. It is indeed sad that the descriptions of these exhibits cannot be given, for it was found necessary in certain cases to transform, for reasons of convenience, a communication that was offered as a paper, into an exhibit, with the result that now there will be found in the *Proceedings* no detailed account of many communications of quality. The forgiveness of those thus affected is sought.

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PROGRAMME

(As has already been stated, there was much alteration of the programme of Sunday and the following days. Nevertheless, though the times were changed, that which follows is substantially an accurate record.)

SYNOPSIS

WEDNESDAY, 23 AUGUST	THURSDAY, 24 AUGUST	FRIDAY, 25 AUGUST
10.30 a.m. PLENARY SESSION McEwan Hall.	9.15 a.m. I. Physiological Genetics (C). Zoology 1. II. Livestock Improvement in the Tropics (D). Geology 1. 10.00 a.m.–12.00 noon Blood-grouping, Taste-testing, etc. G. L. Taylor and colleagues. Zoology Department. 10.00 a.m.–6.00 p.m. Demonstrations and Exhibits. Zoology and Engineering Depts. The Garden: Genetics Dept.	9.15 a.m. I. Plant Breeding (E). Zoology 1. II. Mental Inheritance (F). Engineering 1. III. Artificial Insemination (D). Geology 1. 10.00 a.m.–6.00 p.m. Demonstrations and Exhibits. Zoology and Engineering Depts. The Garden: Genetics Dept.
2.15 p.m. I. Gene and Chromosome Theory (A, B). Zoology 1. II. Livestock Improvement (D). Geology 1. III. Abnormal Human Characters (F). Engineering 1.	2.15 p.m. I. Genetics in Relation to Evolution and Systematics (G). Zoology 1. II. Livestock Improvement in the Tropics (D). Geology 1. III. Growth, normal and abnormal (I). Zoology 2.	2.15 p.m. I. Radiation Effects (A, B). Zoology 1. II. Varietal Trials (E, H). Geology 1. III. Feeblemindedness (F). Engineering 1. IV. Hybridization (G). Chemistry 2. V. Growth (I). Zoology 2. 2.45 p.m. VI. Cytoplasmic Heredity (C). Chemistry 1.
6.00 p.m. Lecture: Max Hartmann. Zoology 1.	6.00 p.m. Lecture: Sir Daniel Hall. Zoology 1.	6.00 p.m. Lecture: C. W. Metz. Zoology 1.
9.00 p.m. Civic Reception by the Lord Provost, Magistrates and Council of the City of Edinburgh. Assembly Rooms.	9.00 p.m. Group Meetings Zoology Dept.: Cytology. Mouse. Human Heredity. Plant Geneticists. Genetics Dept.: Nominating and Resolutions Committees.	9.00 p.m. Reception by His Majesty's Government. Rooms of the Royal Scottish Academy.

SATURDAY, 26 AUGUST	MONDAY, 28 AUGUST	TUESDAY, 29 AUGUST	WEDNESDAY, 30 AUGUST
9.15 a.m. I. Radiation Effects (A, B) Zoology 1. II. Sex (C) Geology 1. III. Statistics and Animal Experimentation (D, H). Genetics. IV. Disease and Vigour (E). Chemistry 1. V. Blood Groups (F). Engineering 1. VI. Comparative Genetics (G). Chemistry 2. VII. Growth (I). Zoology 2. 10.00 a.m.–6.00 p.m. Demonstrations and Exhibits. Zoology and Engineering Depts. The Garden: Genetics Dept.	9.15 a.m. I. Structural Changes (A, B). Zoology 1. II. Embryological Mechanisms (C). Geology 1. III. Milk Yield (D). Genetics. IV. Cereals (E). Chemistry 1. V. Selection in Human Populations (F). Engineering 1. VI. Micro-evolution (G). Chemistry 2. 10.00 a.m.–6.00 p.m. Demonstrations and Exhibits. Zoology and Engineering Depts. The Garden: Genetics Dept.	9.15 a.m. I. Meiosis (B). Zoology 1. II. Physiological Characters (C). Chemistry 1. III. Small Mammals (D). Genetics. IV. Reproduction and Species Hybrids (E). Chemistry 2. V. Abnormal Human Characters (F). Engineering 1. VI. Experimental and Wild Populations (G). Geology 1. Section D. Excursion to West of Scotland. 10.00 a.m.–6.00 p.m. Demonstrations and Exhibits. Zoology and Engineering Depts. The Garden: Genetics Dept.	9.15 a.m. I. Gene Mutation (A). Zoology 1. III. Hormonal Relations (C). Chemistry 1. IV. Nutrition and Genetics (D). Genetics. V. Plant Improvement (E). Chemistry 2. VI. Human Characters (F). Engineering 1. VII. Polyploidy and Reproductive Mechanisms (G). Geology 1. 10.30 a.m. II. Cytological Analysis (B). Zoology 2.
2.15 p.m. I. Structural Changes (A, B). Zoology 1. II. Sex (C). Geology 1. III. Inbreeding (D). Genetics. IV. Principles of Plant Breeding (E). Chemistry 1. V. Statistical Methods in Human Genetics (F, H). Engineering 1. VI. Comparative Genetics and Evolution (G). Chemistry 2. VII. Growth (I). Zoology 2. 6.00 p.m. Lecture: O. Vogt. Zoology 1.	2.15 p.m. I. Meiosis (B). Zoology 1. II. Embryological Mechanisms (C). Geology 1. III. Cattle and Sheep (D). Genetics. IIIA. Poultry (D). Zoology 2. IV. Twinning (F). Engineering 1. V. Micro-evolution (G). Chemistry 2. 2.15 p.m.–4.15 p.m. Demonstration on Blood-grouping, Taste-testing, etc. G. L. Taylor and colleagues. Zoology Department. 4.30 p.m. Protein and Virus Studies (A, B). Engineering 1.	2.15 p.m. I. Chromosome Structure (B) Zoology 1. II. Physiological Characters (C). Chemistry 1. III. Small Mammals (D). Genetics. IV. Reproduction and Species Hybrids (E). Chemistry 2. V. Abnormal Human Characters (F). Engineering 1. VI. Experimental and Wild Populations (G). Geology 1. VII. Growth (I). Zoology 2. 5.30 p.m. PLENARY SESSION Geology 1.	2.15 p.m. I. Gene Mutation (A). Zoology 1. II. Cytological Analysis (B). Zoology 2. III. Biochemical (C). Chemistry 1. IV. Pig (D). Genetics. V. Genetic Analysis (E). Chemistry 2. VI. Human Characters (F). Engineering 1. VII. Polyploidy and Reproductive Mechanisms (G). Geology 1.
8.30 p.m. Group Meetings. Chemistry Department. Colchicine. Human Heredity.	8.30 p.m. Protein and Virus Studies (*cont.*). Engineering 1.	8.30 p.m. Reception: Zoological Society of Scotland. Zoological Park.	

EXCURSIONS

TUESDAY, 22 Aug. 9.00 p.m. Informal reception in Reception Room.

WEDNESDAY, 23 Aug. 2.30 p.m. Sightseeing tours round the city.

THURSDAY, 24 Aug. 2.30 p.m. Sightseeing tours round the city. Entertainment for Ladies by the Ladies' Committee.

FRIDAY, 25 Aug. 9.15 a.m. Section D. Excursion to University Farms.

FRIDAY, 25 Aug. 2.30 p.m. Tour to Scott Country.

SATURDAY, 26 Aug. 2.15 p.m. Tour to the Forth Bridge and Roslin.

SATURDAY, 26 Aug. 4.30 p.m. Entertainment for Ladies by the Ladies' Committee: Zoological Park.

SUNDAY, 27 Aug. 10.40 a.m. All day tour by rail.

SUNDAY, 27 Aug. 9.00 p.m. Informal gathering in Reception Room.

MONDAY, 28 Aug. 2.30 p.m. Tour to Pentland Hills, Peebles, etc.

TUESDAY, 29 Aug. 9.00 a.m. All day excursion by rail, coach and steamer to Kyles of Bute and Clyde Lochs.

TUESDAY, 29 Aug. 9.15 a.m. Section D. All day excursion to farms in West of Scotland.

TUESDAY, 29 Aug. 2.30 p.m. Entertainment for Ladies by the Ladies' Committee: Royal Botanic Gardens.

WEDNESDAY, 30 Aug. 9.00 a.m. All day excursion to Trossachs, etc.

WEDNESDAY, 30 Aug. 3.00 p.m. Entertainments for Ladies by Ladies' Committee: Visits to University Departments.

MEETINGS

WEDNESDAY, 23 AUGUST

9.00 a.m.—Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room (Geology Department).

10.30 a.m.—PLENARY SESSION of the Congress in the McEwan Hall, Treviot Place. *Chairman:* OTTO L. MOHR, Chairman of the International Committee.

Address of welcome by BAILIE EDWARD, representing the City of Edinburgh.

Address of welcome by SIR THOMAS HUDSON BEARE, Dean of the Faculty of Science, representing the University of Edinburgh.

The Congress will elect its Vice-Presidents.

The Congress will elect a committee to nominate members of the permanent International Committee and to report to the Plenary Session of 29 August.

The Congress will give to this International Committee so appointed, authority to select the place and date of the next Congress.

The Congress will elect a committee to prepare resolutions to be presented at the Plenary Session of 29 August.

The Chairman will invite Official Representatives to present their credentials at the Congress Office before 27 August.

The Chairman will address the Congress.

The Session will adjourn until 5.30 p.m. on 29 August.

2.15 p.m. THEME 1 — SECTIONS A AND B

GENE AND CHROMOSOME THEORY

Zoology Lecture Theatre. *Chairman:* O. L. MOHR.

STADLER, L.J.—"Genetic Studies with Ultra-violet Radiation."

PAINTER, T.S.—"Salivary Chromosome Structure and the Genes."

DARLINGTON, C.D.—"The Prime Variables of Meiosis."

TIMOFÉEFF-RESSOVSKY, N.W.—"Mechanismus der Punktmutationen."

MULLER, H.J.—"The Mechanism of Structural Change in Chromosomes."

2.15 p.m. THEME 2 — SECTION D

LIVESTOCK IMPROVEMENT

Geology Lecture Theatre. *Chairman:* SIR ROBERT GREIG.

MCPHEE, H.C.—"Recent Attempts to Co-ordinate Genetic Research on Farm Animals in the U.S.A."

BONNIER, G.—"Theoretical and Practical Possibilities of Genetics in Contributing to the Improvement of Livestock."

HIRSCHFELD, W.K. and PLANK, G.M. VAN DER.—"Genetics and Animal Breeding."

HAGEDOORN, A.L.—"Concentration of Effort in Selection by Means of the 'Nucleus Plan' of Breeding Farm Livestock."

2.15 p.m. THEME 3 — SECTION F

ABNORMAL HUMAN CHARACTERS

Engineering Lecture Theatre. *Chairman:* B. S. BURKS.

LENZ, F.—"Was bedeutet 'Erblich' und 'Nichterblich' beim Menschen?"

PENROSE, L.S.—"Maternal Age, Order of Birth and Developmental Abnormalities."

MUNRO, T.A., PENROSE, L.S. and TAYLOR, G.L.—"A Study of the Linkage Relationship between the Genes for Phenylketonuria and the ABR Allelomorphs in Man."

MUNRO, T.A.—"The Genetics of Phenylketonuria."

LUNDHOLM, I.—"Inheritance of Hypochromic Anaemia."

NACHTSHEIM, H.—"Krampfbereitschaft und Genotypus nach Untersuchungen am Kaninchen."

SANDERS, J.—"A Family with Pick's Disease."

FERRIMAN, D.—"The Genetics of True Oxycephaly and Acrocephalosyndactyly."

6.00 p.m. Lecture: MAX HARTMANN.

"Das Wesen und die stofflichen Grundlagen der Sexualität."

Zoology Lecture Theatre. *Chairman:* F. BALTZER.

THURSDAY, 24 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 — SECTION C

PHYSIOLOGICAL GENETICS

Zoology Lecture Theatre. *Chairman:* MAX HARTMANN.

WRIGHT, SEWALL.—"A Quantitative Study of the Interactions of the Major Colour Factors of the Guinea-pig."

BEADLE, G.W.—"Genetic Control of the Production and Utilization of Hormones."

BALTZER, F.—"Ueber die Rolle des Kerns in der Embryonalentwicklung: Typen der Letalität und Austauschbarkeit artverschiedener Kerne bei Bastarden."
WETTSTEIN, F.v.—"Ueber cytoplasmatische Vererbung und die Zusammenwirkungen von Kern und Cytoplasma."

9.15 a.m. THEME 2 SECTION D

LIVESTOCK IMPROVEMENT IN THE TROPICS

Geology Lecture Theatre. *Chairman:* Sir ARTHUR OLVER.
BISSCHOP, J.H.R.—"Bionomic Studies on Indigenous and Exogenous Cattle in the Semi-arid Regions of the Union of South Africa."
NICHOLS, J.E.—"Genotype and Environment. Some Aspects of Selection of Merino Stock for Wool Production under Pastoral Conditions."
RHOAD, A.O.—"A Method of Assaying the Genetic Differences in the Adaptability of Cattle to Tropical and Subtropical Climates."
MANRESA, M., REYES, N.C., GOMEZ, F., ZIALCITA, L.P. and FALCON, P.R.—"The Influence of Atmospheric Temperature upon Haemoglobin and other Constituents of the Blood of Cattle."

10.00 a.m.–12.00 a.m. Blood-grouping, Taste-testing, etc. G.L. TAYLOR and colleagues. Zoology Department.

10.00 a.m.–6.00 p.m. Demonstrations and Exhibits in the Zoology and Engineering Departments. The Garden: Genetics Department.

2.15 p.m. THEME 1 SECTION G

GENETICS IN RELATION TO EVOLUTION AND SYSTEMATICS

Zoology Lecture Theatre. *Chairman:* A. ERNST.
DOBZHANSKY, TH.—"On the Genetic Structure of Natural Populations of *Drosophila*."
TISCHLER, G.—"Die Bedeutung chromosomaler Rassendifferenzen für Systematik und Pflanzengeographie."
HUXLEY, J.S.—"Evolutionary Genetics."
TURRILL, W.B.—"Taxonomy and Cytogenetics in Plants."
HARLAND, S.C.—"Genetical Studies in the Genus *Gossypium* and their Relationship to Evolutionary and Taxonomic Problems."

2.15 p.m. THEME 2 SECTION D

LIVESTOCK IMPROVEMENT IN THE TROPICS (*cont.*)

Geology Lecture Theatre. *Chairman:* Sir ARTHUR OLVER.
FRENCH, M.H.—"Cattle Breeding in Tanganyika Territory and Some Development Problems Encountered."
KHISHIN, A.F. el—"The Present Conditions of Animal Breeding and Husbandry in Egypt."
STEWART, J.L.—"Livestock Improvement in the Northern Territories of the Gold Coast."
MURARI, SRI T.—"Cross-breeding Experiments with Cattle in the Madras Presidency."
KELLEY, R.B.—"Animal Industries in Tropica Australia."

2.15 p.m. THEME 3 SECTION I

GROWTH, NORMAL AND ABNORMAL

Zoology Lecture Theatre No. 2. *Chairman:* E. B. FORD.
CRAMER, W. and HORNING, E.S.—"On the Association in Inbred Strains of Mice between Brown Degeneration of the Adrenals and the Incidence of Mammary Cancer."
KREYBERG, L.—"The Relationship between Brown Degeneration of the Adrenals and Breast Cancer in Mice."
BONSER, G.M.—"Presence of Brown Degeneration in the Adrenals of Mice of Several Strains."
HOWARD, A. and HUSKINS, C.L.—"Chromosome Studies in Mice."
WOOLLEY, G.W.—"The Effect of Male Secretions upon Tumour Incidence in Mice."
GORER, P.A.—"The Question of Dominance in Spontaneous Cancer."

6.00 p.m. Lecture: Sir DANIEL HALL.
"How Does the Plant Breeder go to Work?"
Zoology Lecture Theatre.
Chairman: Sir WILLIAM WRIGHT SMITH.

9.00 p.m. GROUP MEETINGS.
Cytology Films. Zoology Lecture Theatre No. 1.
Mouse. Zoology Lecture Theatre No. 2.
Committee Meeting: the International Group for Human Heredity. Zoology Colloquium Room.
Meeting of Plant Geneticists: Convener: O. H. FRANKEL. Zoology Department.
Meetings of the Nominating and Resolutions Committees. Genetics Department.

FRIDAY, 25 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 SECTION E

PLANT BREEDING IN THE LIGHT OF GENETICS

Zoology Lecture Theatre. *Chairman:* R. A. EMERSON.
LINDSTROM, E.W.—"Analysis of Modern Maize Breeding Principles and Methods."
MANGELSDORF, P.C.—"The Origin of Maize."
RASMUSSON, J.—"Quantitative Inheritance in Root Crops."

9.15 a.m. THEME 2 SECTION F

MENTAL INHERITANCE IN MAN

Engineering Lecture Theatre. *Chairman:* E. FISCHER.
HOGBEN, L.T.—"Genetic Variation and Human Intelligence."
POHLISCH, K.—"Die Vererbbarkeit der Geisteskrankheiten."
ROBERTS, J.A.F.—"Inheritance of Mental Deficiency."
DAHLBERG, G.—"Rare Psychological Defects from the Point of View of the Population."

9.15 a.m. THEME 3 SECTION D

ARTIFICIAL INSEMINATION

Geology Lecture Theatre. *Chairman:* E. P. CATHCART.
BONADONNA, T.—"Ricerche sulla fecondazione artificiale in Italia."
PHILLIPS, R.W., SCHOTT, R.G., TERRILL, C.E. and GILDOW, E.M.—"Long-range Transportation of Ram Semen for Use in Artificial Insemination."
TEODOREANU, N.—"Studies in Artificial Insemination of Sheep."
OLBRYCHT, T.M.—"The Lwów Methods of Artificial Insemination." (Film.)
ANDERSON, J.—"Artificial Insemination of Sheep and Cattle in Kenya."
EDWARDS, J. and WALTON, A.—"Problems of Semen Production related to Artificial Insemination."

10.00 a.m.–6.00 p.m. Demonstrations and Exhibits in the Zoology and Engineering Departments. The Garden: Genetics Department.

FRIDAY, 25 AUGUST (*continued*)

2.15 p.m. THEME 1 SECTIONS A AND B

RADIATION EFFECTS AND THE MECHANISM OF STRUCTURAL CHANGE IN CHROMOSOMES

Zoology Lecture Theatre. *Chairman:* L. J. STADLER.

CATCHESIDE, D.G.—"The Mechanism of Radiation-induced Chromosome Rearrangements."

FABERGÉ, A.C.—"An Experiment on Chromosome Fragmentation by X-rays in *Tradescantia*."

MARSHAK, A.—"Chromosome Structure in Meiosis and Mitosis."

CAMARA, A.—"The Effect of X-radiation on the Chromosomes of *Aloë arborescens*."

SIDKY, A.R.—"Translocation between Sperm and Egg Chromosomes as Evidence that Breakage Precedes Union."

2.15 p.m. THEME 2 SECTIONS E AND H

VARIETAL TRIALS AND SELECTIVE IMPROVEMENT

Geology Lecture Theatre. *Chairman:* E. W. LINDSTROM.

YATES, F.—"Modern Experimental Design and its Function in Plant Selection."

RASMUSSON, J.—"Field Trials in Sugar Beet Breeding."

GOULDEN, C.H.—"Problems in Plant Selection."

DAY, B.B. and AUSTIN, L.—"The Use of the Three-dimensional Quasi-factorial Design for Testing a Large Number of Ponderosa Pine Progenies."

HOBLYN, T.N.—"Testing New Varieties of Fruit Plants."

PANSE, V.G.—"The Inheritance of Quantitative Characters and Plant Breeding."

MATHER, K.—"Selection for Polygenic Characters."

2.15 p.m. THEME 3 SECTION F

FEEBLEMINDEDNESS

Engineering Lecture Theatre. *Chairman:* H. TOMASSON.

MURPHY, D.P.—"Reproductive Characteristics of Parents of Congenitally Malformed Children."

BRUGGER, C.—"The Genetic Uniformity of Mental Deficiency without Marked Physical Signs."

FRETS, G.P.—"Families with Feeblemindedness."

BERRY, R.J.A.—"An Investigation into the Mental States of the Parents and Sibs of 1050 Mentally Defective Persons."

2.15 p.m. THEME 4 SECTION G

HYBRIDIZATION

Chemistry Lecture Theatre No. 2.

Chairman: A. L. HAGEDOORN.

FEDERLEY, H.—"Hybridization between Different Species and Races of Lepidoptera with Different Chromosome Number."

CAROTHERS, E.E.—"Interspecific Grasshopper Hybrids."

COUSIN, G.—"Analyse biométrique d'une hybridation interspécifique chez les Gryllides."

PATTERSON, J.T., STONE, W. and GRIFFEN, A.B.—"Crosses between Members of the *Drosophila virilis* Group."

GHIGI, A.—"Incroci interspecifici nei Fasiani."

CAVAZZA, F.—"Alcune osservazioni sull' ibridismo interspecifico dei Mammiferi."

2.15 p.m. THEME 5 SECTION I

GROWTH, NORMAL AND ABNORMAL

Zoology Lecture Theatre No. 2.

Chairman: N. DOBROVOLSKAIA-ZAVADSKAIA.

MACKLIN, M.T.—"An Analysis of Tumours in Monozygous and Dizygous Twins."

LEMSER, H.—"Hypophysentumor und Zwillingsdiagnose."

GEYER, H.—"Die Erbpathologie der Geschwülste des Zentralnervensystems und seiner Hüllen."

BAGG, H.J.—"The Selection of Genetic Material for the Study of the Inheritance of Mammary Tumours in Mice and Rats."

GORER, P.A.—"Transplantation and the Differentiation of the Malignant Cell."

PYBUS, F.C. and MILLER, E.W.—"Hereditary Bone Tumours and Oestrone."

2.45 p.m. THEME 6 SECTION C

CYTOPLASMIC HEREDITY

Chemistry Lecture Theatre No. 1.

Chairman: FR. v. WETTSTEIN.

MICHAELIS, P.—"Plasmavererbung und Entwicklungsphysiologie."

SIRKS, M.J.—"Genotypical Predetermination."

6.00 p.m. Lecture: C. W. METZ.

"Species Hybrids, Evolutionary Chromosome Changes, and the Mechanism of Chromosome Rearrangement in *Sciara*."

Zoology Lecture Theatre. *Chairman:* Ö. WINGE.

SATURDAY, 26 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 SECTIONS A AND B

RADIATION EFFECTS AND THE MECHANISM OF STRUCTURAL CHANGE IN CHROMOSOMES (*cont.*)

Zoology Lecture Theatre. *Chairman:* L. J. STADLER.

JONES, D.F.—"Segmental Exchange in Somatic Cells of Maize."

WHITING, A.R.—"Susceptibility to X-rays of Meiotic Stages in Eggs of *Habrobracon*."

HERTWIG, P.—"Erbänderungen bei Mäusen nach Röntgenbestrahlung."

BAUER, H.—"Röntgeninduktion von Chromosomenmutationen bei *Drosophila*."

9.15 a.m. THEME 2 SECTION C

SEX

Geology Lecture Theatre. *Chairman:* H. DE WINIWARTER.

WHITING, P.W.—"The Cytogenetics of Sex-determination."

SHULL, A.F.—"The Nature of the Intermediacy of Adult Intermediate-winged Aphids and its Bearing on the Manner of their Production."

VANDEL, A.—"Génétique de la sexualité chez les Isopodes terrestres."

MONTALENTI, G.—"Ricerche quantitative sull' azione dei geni della striatura (barring) nelle penne maschili femminili dei polli Barred Plymouth Rocks."

DANTCHAKOFF, V.—"The Genetic Determinants of Sex in the Higher Vertebrates."

9.15 a.m. THEME 3 SECTIONS D AND H

STATISTICS AND ANIMAL EXPERIMENTATION

Genetics Lecture Theatre. *Chairman:* J. F. TOCHER.

YATES, F.—"Statistical Aspects of Animal Experimentation."

BERGE, S.—"On the Number of Offspring Required in Genetical Experiments with Slow-breeding Animals."

LUSH, J.L.—"Methods of Measuring the Heritability of Individual Differences among Farm Animals."

9.15 a.m. THEME 4 — SECTION E

DISEASE AND VIGOUR

Chemistry Lecture Theatre No. 1. *Chairman:* D. F. JONES.

SINGLETON, W.R.—"Hybrid Vigour and its Utilization in Sweet Corn Breeding."

JENKINS, M.T.—"The Segregation of Genes Affecting Yield of Grain in Maize."

SALAMAN, R.N.—"Breeding for Immunity to Blight and other Diseases in the Potato."

MÜLLER, K.O.—"Physiologisch-genetische Untersuchungen zur Analyse der Phytophthora-Resistenz der Kartoffel."

WALKER, J.C.—"Disease Resistance in Crucifers."

JAGGER, I.C. and WHITAKER, T.W.—"The Inheritance of Immunity to Mildew (*Bremia lactucae*) in Lettuce."

CREPIN, C., BUSTARRET, J. and CHEVALIER, R.—"Création pour la France de blés résistants à la Carie."

9.15 a.m. THEME 5 — SECTION F

BLOOD GROUPS

Engineering Lecture Theatre. *Chairman:* R. A. FISHER.

FRIEDENREICH, V.—"Genetical Problems in Recent Research in Blood Groups."

TAYLOR G.L. and PRIOR, A.M.—"The Distribution of the *M* and *N* Factors in Random Samples of Different Races."

GATES, R.R.—"Blood Groups and Race."

TURPIN, R., PITON, J. and CARATZALI, A.—"Recherche sur les corrélations leucocytaires des jumeaux."

FINNEY, D.J.—"An Apparent Linkage of the OAB Blood Groups with Allergic Disease."

9.15 a.m. THEME 6 — SECTION G

COMPARATIVE GENETICS AND EVOLUTION

Chemistry Lecture Theatre No. 2. *Chairman:* H. FEDERLEY.

ERNST, A.—"Heterostylie als Problem der Evolution."

BOYDEN, A.A.—"Genetics and Animal Relationship."

EYSTER, W.H.—"Genetic Study in the Genus *Tagetes*."

9.15 a.m. THEME 7 — SECTION I

GROWTH, NORMAL AND ABNORMAL

Zoology Lecture Theatre No. 2. *Chairman:* J. P. LOCKHART-MUMMERY.

STRONG, L.C.—"Cancer of the Mammary Gland in Mice. Is it Genetic, Congenital, or Acquired?"

DOBROVOLSKAIA-ZAVADSKAIA, N.—"Heredity and Environmental Factors in the Origin of Different Cancers."

CURTIS, M.R. and DUNNING, W.F.—"Host Constitution and the Incidence of Chemically-induced Tumours."

BONSER, G.M.—"The Effect of Genetic Constitution in Determining the Response of the Animal to Carcinogenic Agents."

ANDERVONT, H.B.—"The Use of Inbred Strains of Mice in Experimental Cancer."

BAMBER, R.C.—"Brown Degeneration of the Adrenal Gland in Mice."

10.00 a.m.–6.00 p.m. Demonstrations and Exhibits in the Zoology and Engineering Departments. The Garden: Genetics Department.

2.15 p.m. THEME 1 — SECTIONS A AND B

STRUCTURAL CHANGES AND POSITION EFFECT IN FREE AND CHROMOCENTRAL REGIONS

Zoology Lecture Theatre. *Chairman:* H. BAUER.

DEMEREC, M.—"The Nature of Changes in the White-Notch Region of the X-chromosome of *Drosophila melanogaster*."

SUTTON, E.—"The Structure of Euchromatic and Heterochromatic Translocations in the Salivary Gland Chromosomes of *Drosophila melanogaster*."

KAUFMANN, B.P.—"Distribution of Induced Breaks along the X-chromosome of *Drosophila melanogaster*."

2.15 p.m. THEME 2 — SECTION C

SEX (*cont.*)

Geology Lecture Theatre. *Chairman:* M. CAULLERY.

QUINTANILHA, A.—"Genetical Work on Basidiomycetes."

PEKLO, J.—"Relative Sexuality in *Fomes pinicola*."

SINGH, B.N.—"Certain Aspects of the Physiology of Sex in Higher Plants."

GOTTSCHEWSKI, G.—"Das Geschlechtverhältniss in Bastard-Kreuzungen von *D. pseudo-obscura*."

WHITING, P.W.—"Sex Determination in *Habrobracon*."

2.15 p.m. THEME 3 — SECTION D

INBREEDING, LETHALS AND DEFECTS

Genetics Lecture Theatre. *Chairman:* J. HAMMOND.

EATON, O.N.—"The Effect of Crossing Inbred Lines of Guinea-pigs upon the Characteristics of the Hybrids."

ABDERHALDEN, E. and HERRE, W.—"Die Anwendung der Abwehrproteinase-Reaktion für Fragen der Vererbung."

PRAWOCHEŃSKI, R.—"Some New Lethal Factors in the Horse."

JOHANSSON, I.—"Variations in the Manifestation of Lethal Characters in the Swedish Breeds of Cattle."

ADDINGTON, L.H. and CUNNINGHAM, O.C.—"An Inherited Di-mamilla in Milk Goats."

2.15 p.m. THEME 4 — SECTION E

PRINCIPLES OF PLANT BREEDING

Chemistry Lecture Theatre No. 1. *Chairman:* E. TSCHERMAK VON SEYSENEGG.

ÅKERMAN, Å.—"Spring-wheat Breeding in Sweden."

FRANKEL, O.H.—"Some Reflections on Breeding Wheat for Baking Quality."

PHILP, J.—"On Wheat Breeding and Genetics."

LOVE, R.M.—"The Role of Cytology in Wheat Improvement."

BRIGGS, F.N.—"The Use of the Backcross in Plant Breeding."

HUTCHINSON, J.B.—"The Genetic Interpretation of Plant-breeding Problems."

WHITE, O.E.—"Genes, Species, Variability and Plant Breeding."

SHEN, T.H.—"Adaptability of Wheat Varieties in Relation to the Various Regions and Breeding Centres in China."

2.15 p.m. THEME 5 — SECTIONS F AND H

STATISTICAL METHODS IN HUMAN GENETICS

Engineering Lecture Theatre. *Chairman:* SEWALL WRIGHT.

FISHER, R.A.—"The Detection and Measurement of Linkage in Man."

HALDANE, J.B.S.—"New Data on Partial Sex-linkage."

SATURDAY, 26 AUGUST (*continued*)

GINI, C.—"L'importanza relativa dei fattori ereditari e non ereditari nel determinare l'eterogeneità di una generazione."
DAHLBERG, G.—"A Method of Deciding Dominance or Recessivity of Polymeric Inheritance."
HOGBEN, L.T.—"Biological Models for Statistical Treatment of Human Genetics."

2.15 p.m. THEME 6 SECTION G

COMPARATIVE GENETICS AND EVOLUTION (*cont.*)

Chemistry Lecture Theatre No. 2. *Chairman:* A. GHIGI.
IBSEN, H.L. and BOGART, R.—"Pigmentation in Relation to Colour Inheritance in Mammals."
BLARINGHEM, L.—"Hérédité et Évolution chez les Plantes."
MARCHLEWSKI, T.—"Change of Dominance in Canine Colour Genetics."
MENSINKAI, S.W.—"Evolution in the Genus *Allium*."

2.15 p.m. THEME 7 SECTION I

GROWTH, NORMAL AND ABNORMAL

Zoology Lecture Theatre No. 2. *Chairman:* L. KREYBERG.
FORD, E.B.—"The Genetics of Growth and Differentiation."
ERNST, A.—"Vererbung teratologischer Merkmale durch labile Gene."
LOCKHART-MUMMERY, J.P.—"Somatic Mutation as a Cause of Tumours."
LUDFORD, R.J.—"Can Somatic Cell Mutations Explain the Properties of Malignant Cells?"

6.00 p.m. Lecture: O. VOGT.
"Variation im Lichte topistischer Krankheiten."
Zoology Lecture Theatre. *Chairman:* R. J. A. BERRY.

8.30 p.m. GROUP MEETINGS. CHEMISTRY DEPARTMENT.
Colchicine Group. Round-table discussion to be opened by BLAKESLEE, A.F.—"The Induction of Polyploids and their Genetic Significance."
Open Meeting of the International Group for Research in Human Heredity. Chemistry Lecture Theatre No. 1.

SUNDAY, 27 AUGUST

All day tour by rail to Stirling, Callander, Balquhidder, Lochearnhead, Comrie, Crieff, Gleneagles, Dunblane, Stirling, etc.

9.00 p.m. Informal gathering in the Reception Room. Music. Light Refreshments.
Discussion on Teaching Methods: (*a*) the statistical requirements of students of Genetics (opened by C.D. DARLINGTON); (*b*) the use of models in the teaching of Cytogenetics (opened by J.S. HUXLEY). Genetics Lecture Theatre.

MONDAY, 28 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 SECTIONS A AND B

STRUCTURAL CHANGES AND POSITION EFFECT IN FREE AND CHROMOCENTRAL REGIONS (*cont.*)

Zoology Lecture Theatre. *Chairman:* H. BAUER.
OLIVER, C.P.—"The Relationship between Chromosomal Disarrangements and a Morphological Variant in *Drosophila melanogaster*."
SCHULTZ, J.—"The Function of Heterochromatin."

9.15 p.m. THEME 2 SECTION C

EMBRYOLOGICAL MECHANISMS

Geology Lecture Theatre. *Chairman:* J. NEEDHAM.
LANDAUER, W.—"Teratological Correlations and the Mechanism of Gene Expression."
RUSSELL, W.L.—"Physiological Genetics of Guinea-pig Coat Colour."
BONNEVIE, K.—"The Manifestation of Hydrocephalus in Mice."
HADORN, E. and RIS, H.—"Zur Entwicklungsphysiologie einer Letalmutante von *Drosophila melanogaster*."
QUISENBERRY, J.H.—"Relationship of Genetic and Nutritional Factors in the Production of Developmental Anomalies."
STEINBERG, A.G.—"The Growth Curves of Bar and Wild-type Eye-disks of *Drosophila melanogaster*."
CHILD, G.P.—"The Effect of Increasing Time of Development at Constant Temperature on the Wing Size of Vestigial of *Drosophila melanogaster*."

9.15 a.m. THEME 3 SECTION D

INHERITANCE OF MILK YIELD

Genetics Lecture Theatre. *Chairman:* LORD ROWALLAN.
KRÜGER, L.—"Die Bestimmung von Leistungswert, Erbwert, Erbanlagen und Erbquanten bei der Milchleistung."
LÖRTSCHER, H.—"Ursachen der Variation der Jahresdurchschnitte einer Milchviehherde."
CSUKÁS, Z.—"The Genetics of the Lactation Curve."
WARD, A.H. and CAMPBELL, J.T.—"Evaluation of Dairy Sires in New Zealand."
MARCHLEWSKI, T.—"Indications of Sex-linkage in Milk-yield Inheritance in Cattle."
ASHOUR, A.M.M.—"The Use of Records in Estimating the Productive Ability of Dairy Cows."

9.15 a.m. THEME 4 SECTION E

CEREALS

Chemistry Lecture Theatre No. 1.
Chairman: N. H. NILSSON-EHLE.
BELL, G.D.H.—"Cereal Breeding and Research at the Cambridge University Plant Breeding Station."
ROBERTSON, D.W.—"Studies of Barley Genetics in Colorado."
JONES, E.T.—"A Comparison of the Segregation of Wild *v.* Cultivated Base in the Grain of Diploid, Tetraploid and Hexaploid Species of Oats."
ELLISON, W.—"The Cytology of certain Diploid and Tetraploid *Avena* Hybrids."
TAVČAR, A.—"Inheritance of 2-, 3-, 4-, and 6-articulate Leaf Whorls in *Zea Mays* L."
GÖKĞÖL, M.—"Zur Frage des Ursprungsgebietes der Weizen."

9.15 a.m. THEME 5 SECTION F

SELECTION IN HUMAN POPULATIONS

Engineering Lecture Theatre. *Chairman:* C. GINI.
HALDANE, J.B.S.—"Natural Selection in Man."
CHARLES, E.—"Contemporary Trends in Differential Fertility."
PRICE, B.—"An Interpretation of Differential Birth Rate Statistics."
GINI, C.—"Considerazioni a cui danno luogo i caratteri concatenati a seguito dell' intercambio."
VERSCHUER, O.v.—"Bemerkungen zur Gen-Analyse beim Menschen."

9.15 a.m. THEME 6 SECTION G

MICRO-EVOLUTION

Chemistry Lecture Theatre No. 2. *Chairman:* G. TISCHLER.

PLOUGH, H.H.—"The Influence of Temperature in Evolution as shown by Studies of Lethal Mutation in *Drosophila*."

IVES, P.T.—"A High Frequency of Lethal Mutations in a Wild Population of *Drosophila*."

LAMPRECHT, H.—"The Limit between *Phaseolus vulgaris* and *Ph. multiflorus* from the Genetical Point of View."

MICZYŃSKI, K.—"The Inheritance of Some Characters in the Intervarietal Crosses of *Aegilops*."

RILEY, H.P.—"Morphogenesis of Flower Parts in Two Species of *Iris*."

10.00 a.m.–6.00 p.m. Demonstrations and Exhibits in the Zoology and Engineering Departments. The Garden: Genetics Department.

2.15 p.m. THEME 1 SECTION B

MEIOSIS, SEGREGATION AND CROSSING-OVER

Zoology Lecture Theatre. *Chairman:* Th. DOBZHANSKY.

WHITE, M.J.D.—"Chromosomal Evolution and the Mechanism of Meiosis in Praying Mantids."

KOLLER, P.C.—"Crossing-over in the Sex-chromosomes of Mammals."

SANSOME, E.R.—"Abnormal Meiosis in *Pisum sativum*."

PÄTAU, K.—"Der Paarungskoefficient."

HUSKINS, C.L. and NEWCOMBE, H.B.—"Chromatid and Chiasma Interference in *Trillium erectum* L."

2.15. THEME 2 SECTION C

EMBRYOLOGICAL MECHANISMS (*cont.*)

Geology Lecture Theatre. *Chairman:* K. BONNEVIE.

WADDINGTON, C.H.—"The Mechanism of the Genetic Control of Development."

POULSON, D.F.—"The Developmental Effects of a Series of *Notch* Deficiencies in the X-chromosome of *Drosophila melanogaster*."

REED, S.C.—"Interaction between the Autosomes of *D. melanogaster* as Measured by Viability and Rate of Development."

REED, S.C. and HENDERSON, J.M.—"Determination of Hair Pigments."

CHILD, G.P., BLANC, R. and PLOUGH, H.H.—"The Effects of High Temperature on the Development of Heterozygous Recessives of *Drosophila melanogaster*."

2.15 p.m. THEME 3 SECTION D

CATTLE AND SHEEP

Genetics Lecture Theatre. *Chairman:* R. G. WHITE.

PONTECORVO, G.—"Problems in Connexion with the Selection of Beef and Draft Cattle."

JONES, I.C.—"Red, Roan and White Coat Colour in Shorthorn Cattle."

DRY, F.W.—"Kemp in the New Zealand Romney."

2.15 p.m. THEME 3*a* SECTION D

POULTRY

Zoology Lecture Theatre No. 2. *Chairman:* C. BONNIER.

LAUPRECHT, E.—"Über die Vererbung des Eigewichtes bei Hühnern."

GHIGI, A.—"Genetica dell' ernia cerebrale nei Polli."

GREENWOOD, A.W.—"A Study of Fecundity in the Domestic Fowl."

HAYS, F.A.—"Inheritance of Comb Type and Earlobe Colour in Rhode Island Reds."

HUTT, F.B.—"The Association of Physiological Traits with Breed Characteristics in the Fowl."

JAAP, R.G.—"Proportional Body Shape and Growth in the Domestic Fowl."

LANDAUER, W.—"The Role of Unspecific Growth Retardation in the Expression of Inherited Traits (Creeper Fowl, etc.)."

2.15 p.m. THEME 4 SECTION F

TWINNING

Engineering Lecture Theatre. *Chairman:* O. v. VERSCHUER.

SLATER, E.—"Inheritance of Twinning."

JENKINS, R.L. and GWIN, J.—"Rigorous Analysis of the Interrelations of the Frequencies of Plural Births."

MALÂN, M.—"Zwillingsuntersuchungen über die Orientierungsfähigkeit."

MURPHY, D.P.—"The Outcome of 625 Pregnancies in Women subjected to Pelvic Radium or Roentgen Irradiation."

CLAUSSEN, F.—"Zur Phänogenese von Missbildungen."

2.15 p.m. THEME 5 SECTION G

MICRO-EVOLUTION

Chemistry Lecture Theatre No. 2. *Chairman:* M. CHRISTOFF.

ZARAPKIN, S.R.—"The Measurement of Divergency."

LARAMBERGUE, M. DE—"Racesaphalliques et euphalliques de *Bulinus contortus*, recherches sur le déterminisme génotypique de l'aphallie."

CLELAND, R.E.—"Analysis of Wild American Races of *Oenothera* (*Onagra*)."

GATES, R.R.—"The Geographical Relationships and Evolution of the Subgenus *Onagra*."

2.15 p.m.–4.15 p.m. Demonstration on Blood-grouping, Taste-testing, etc. G.L. TAYLOR and Colleagues, Zoology Department.

4.30 p.m.–6.30 p.m. SECTIONS A AND B

SESSION ON PROTEIN AND VIRUS STUDIES IN RELATION TO THE PROBLEM OF THE GENE

Engineering Lecture Theatre. *Chairman:* J.B.S. HALDANE.

ASTBURY, W.T.—"Protein and Virus Studies in Relation to the Problem of the Gene."

CROWFOOT, D.—"Recent Work on the Crystalline Proteins and Viruses."

WRINCH, D.M.—"The Fabric Structure of Proteins, with Special Reference to Problems of Cytogenetics."

GULICK, A.—"Analysis of Nuclear Material Obtained by Differential Centrifugation of Finely Powdered Glandular Tissue."

CASPERSSON, T.—"On the Role of the Nucleic Acids in the Cell."

8.30 p.m.–10.30 p.m.

KAUSCHE, G.A.—"Untersuchungen zum Problem der biologischen Charakterisierung phytopathogener Virusarten."

MCKINNEY, H.H.—"Virus Genes."

GOWEN, J.W.—"Behaviour of Viruses and Genes under Similar Stimuli."

L'HERITIER, P. and TEISSIER, G.—"Une monstruosité physiologique héréditaire."

MAZIA, D. and JAEGER, L.—"Nuclease Action, Protease Action, and Histochemical Tests on Salivary Chromosomes of *Drosophila*."

TUESDAY, 29 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 — SECTION B

MEIOSIS (*cont.*)

Zoology Lecture Theatre. *Chairman:* M. M. RHOADES.

LINDEGREN, C.C.—"Excessive Serial Two-strand Crossing-over in *Neurospora crassa*."

LUDWIG, W.—"Bemerkungen zur Chiasmabildung und zur Interferenz."

KÖRÖSY, K. DE—"Outlines of a Theory of Interference."

WEINSTEIN, A.—"The Interrelations of Genetic Functions."

OEHLKERS, F.—"Meiosis und Crossing-over."

9.15 a.m. THEME 2 — SECTION C

PHYSIOLOGICAL CHARACTERS

Chemistry Lecture Theatre No. 1. *Chairman:* A. VANDEL.

WINGE, Ö.—"On Inconstancy in Single Cell Cultures of Micro-organisms owing to Segregation and on Hybridization in Yeast."

CSIK, L.—"Sauerstoffverbrauch der *Drosophila*-Puppen verschiedenen Genotypus."

JUCCI, C.—"Genetica baco da seta."

PLAGGE, E.—"Die Wirkung des Gen-abhängigen a^+-Hormons bei *Ephestia*."

SCHREIBER, G.—"Alcuni aspetti genetici del problema della metamorfosi degli anfibi."

9.15 a.m. THEME 3 — SECTION D

SMALL MAMMALS

Genetics Lecture Theatre. *Chairman:* J. RITCHIE.

BAMBER, R.C.—"A Time Factor in White-spotting in Cats."

GRÜNEBERG, H.—"Inherited Macrocytic Anæmias in the House Mouse."

KOBOZIEFF, N. and POMRIASKINSKY-KOBOZIEFF, N.A.—"Nouvelles recherches sur le mode de transmission héréditaire des anomalies des oreilles chez la Souris: 'abaissement du pavillon' et 'pavillon tronqué'."

STRANDSKOV, H.H.—"Inheritance of Internal Organ and Skeletal Variations in Guinea-pigs."

WILSON, W. KING.—"Alternative Modes of Inheritance of Steel-grey Coat Colour in Rabbits."

9.15 a.m. THEME 4 — SECTION E

REPRODUCTION AND SPECIES HYBRIDS

Chemistry Lecture Theatre No. 2.

Chairman: Sir DANIEL HALL.

CRANE, M.B. and THOMAS, P.T.—"Reproductive Versatility in *Rubus*."

OLAH, L.—"Interspecific Hybrids in the Genus *Phleum*."

LEWIS, D.—"The Relationship between Polyploidy and Fruiting Habit in the Cultivated Raspberry."

LAMM, R.—"Varying Cytological Behaviour in Reciprocal *Solanum* crosses."

GISQUET, P., DUFRENOY, J. and DUSSEAU, A.—"Interspecific Hybrids among *Nicotiana*: Hybrids between *N. Tabacum* var. *purpurea* and *N. petunioides* var. *sylvestris*."

9.15 a.m. THEME 5 — SECTION F

ABNORMAL HUMAN CHARACTERS

Engineering Lecture Theatre. *Chairman:* G. P. FRETS.

HENDERSON, D.K.—"Eugenics and Insanity."

KALLMANN, F.J.—"The Scientific Goal in the Prevention of Hereditary Mental Disease and Racial Inferiority."

TOMASSON, H.—"Investigations on Heredity of Manic-depressive Psychosis in Iceland."

ROBB, R.C.—"The Relative Frequency of Inheritable Disorders among 100,000 Hospitalized Patients."

PATZIG, B.—"Die Schizophrenie als genetisches Problem."

9.15 a.m. THEME 6 — SECTION G

EXPERIMENTAL AND WILD POPULATIONS

Geology Lecture Theatre. *Chairman:* C. S. ELTON.

FORD, E.B.—"A Quantitative Population Study in Butterflies."

EMERSON, S.—"The Distribution of Self-sterility Allelomorphs in a Natural Population."

BARIGOZZI, C.—"Analisi citogenetica di due popolazioni naturali di *Artemia salina*."

ZIMMERMANN, K.—"Some Results of Genetical Analysis in Populations of Wild Rodents."

SPENCER, W.P.—"Ecological Factors and the Distribution of Genes in *Drosophila hydei* Populations."

10.00 a.m.–6.00 p.m. Demonstrations and Exhibits in the Zoology and Engineering Departments. The Garden: Genetics Department.

2.15 p.m. THEME 1 — SECTION B

CHROMOSOME STRUCTURE

Zoology Lecture Theatre. *Chairman:* M. DEMEREC.

HEITZ, E.—"Entwicklung der Frage über die Beziehung zwischen Kernstruktur, Chromosomenstruktur und Genen."

MANTON, I.—"Evidence on Chromosome Structure in *Osmunda*."

SLIZYŃSKA, H. and SLIZYŃSKI, B.M.—"A Salivary Gland Chromosome Map of *Drosophila funebris* Fabr."

BARBER, H.N.—"The Origin and Behaviour of Diplochromosomes."

BERGER, C.A.—"On the Origin and Fate of Different Types of Polyploid Nuclei."

GEITLER, L.—"Polyploide Somakerne und ihre Entstehung durch Endomitose bei Heteropteren."

2.15 p.m. THEME 2 — SECTION C

PHYSIOLOGICAL CHARACTERS (*cont.*)

Chemistry Lecture Theatre No. 1. *Chairman:* C. JUCCI.

SZABÓ, Z.—"The Connection between Genotype and Constitution."

GORDON, C. and SANG, J.H.—"The Effect of Environment on the Exhibition of 'Antennaless' in *D. melanogaster*."

NEEL, J.—"Temperature, Body Size and Character Expression in *Drosophila*."

SCHOENHEIMER, S. GLUECKSOHN.—"On a New Short Tail Mutation in Mice."

SMITH, T.L.—"The Genetics of the Wax Moth, *Galleria mellonella*."

2.15 p.m. THEME 3 — SECTION D

SMALL MAMMALS (*cont.*)

Genetics Lecture Theatre. Round-table discussion.

SMITH, G. ENNIS.—"Fox-breeding: Fundamentals of Line Breeding."

2.15 p.m. THEME 4 SECTION E

REPRODUCTION AND SPECIES HYBRIDS (*cont.*)

Chemistry Lecture Theatre No. 2. *Chairman:* M. J. SIRKS.

TSCHERMAK VON SEYSENEGG, E.—"Weitere Beobachtungen über hybridogene Pseudoparthenogenesis."

THOMPSON, W.P.—"The Frequency of Fertilization and the Nature of Embryo and Endosperm Development in Intergeneric Crosses in Cereals."

ARMSTRONG, J.M., WHITE, W.J., MCLENNAN, H.A. and JOHNSON, L.P.V.—"Genetic Investigations in *Triticum-Agropyron* hybrids."

PETO, F.H.—"Cytology of *Triticum-Agropyron glaucum* Back-crosses."

JANAKI, E.K.—"Triplopolyploidy and the Production of Fertile Intergeneric Hybrids in *Saccharum*."

VANDENDRIES, R. and GAVAUDAN, P.—"Remarques concernant l'action de la Colchicine et de l'Acénaphtène sur quelques organismes inférieurs."

HAIG-THOMAS, R.—"On a Species which Proved to be a Wild Hybrid."

2.15 p.m. THEME 5 SECTION F

ABNORMAL HUMAN CHARACTERS (*cont.*)

Engineering Lecture Theatre.

Chairman: P. J. WAARDENBURG.

SCHADE, H.—"Beitrag zur Feststellung der Häufigkeit von Erbkrankheiten."

ROBERTS, J.A.F.—"Resemblances in Intelligence between Sibs Selected from a Complete Sample of an Urban Population."

MADISSOON, H.—"Sur le caractère héréditaire de l'absence des deux reins."

CLAUSSEN, F.—"Zur Phänogenese von Missbildungen."

2.15 p.m. THEME 6 SECTION G

EXPERIMENTAL AND WILD POPULATIONS (*cont.*)

Geology Lecture Theatre.

Chairman: N. W. TIMOFÉEFF-RESSOVSKY.

JENKIN, T.J.—"Evolution in Wild Populations."

BUZZATI-TRAVERSO, A.—"Genetica di popolazioni nelle Drosophilae italiane."

SPURWAY, H.—"Autosomal Genes collected from Wild Populations of *Drosophila subobscura*."

PHILIP, U.—"A Genetical Analysis of Three Small Populations of *Dermestes vulpinus* F."

2.15 p.m. THEME 7 SECTION I

GROWTH, NORMAL AND ABNORMAL

Zoology Lecture Theatre No. 2.

Chairman: H. B. ANDERVONT.

AUERBACH, C.—"Tests of Carcinogenic Substances in Respect of their Influence on Mutation in *Drosophila melanogaster*."

LAMY, R. and MULLER, H.J.—"Evidence of the Non-Genetic Nature of the Lethal Effect of Radiation of *Drosophila* Embryos."

CRAMER, W.—"Permanent Retardation of the Growth Rate of a Transplantable Mouse Carcinoma induced by Radiation."

STARK, M.B.—"The Origin of Certain Hereditary Tumours in *Drosophila*."

STEIN, EMMY.—"Ueber erbliche, durch Radiumbestrahlung erzeugte Gewebe-Entartung in *Antirrhinum siculum* und in Petunien."

5.30 p.m. PLENARY SESSION of the Congress to receive reports and consider resolutions. Geology Lecture Theatre.

8.30 p.m. Reception by the President and Council of the Zoological Society of Scotland at the Zoological Park, Corstorphine.

WEDNESDAY, 30 AUGUST

9.00 a.m. Congress Office opens. Meeting of the Organizing Subcommittee in the Committee Room.

9.15 a.m. THEME 1 SECTION A

GENE MUTATION

Zoology Lecture Theatre No. 1. *Chairman:* P. W. WHITING.

HOLLAENDER, A.—"Wave-length Dependence of the Production of Mutations in Fungous Spores by Monochromatic Ultra-violet Radiation (2180–3650A)."

KNAPP, E. and SCHREIBER, H.—"Quantitative Analyse der mutationsauslösenden Wirkung monochromatischen U.-V.-Lichtes in Spermatozoiden von *Sphaerocarpus*."

RAYCHAUDHURI, S.P.—"The Validity of the Bunsen-Roscoe Law in the Production of Mutations by Radiation of Extremely Low Intensity."

9.15 a.m. THEME 3 SECTION C

HORMONAL RELATIONS

Chemistry Lecture Theatre No. 1.

Chairman: G. W. BEADLE.

EPHRUSSI, B., VOGT, M. and GOLDSTEIN, L.—"Sur la relation entre la production de l'hormone v^+ et le dosage du gène v^+ chez *Drosophila melanogaster*."

TATUM, E.L., BEADLE, G.W. and CLANCY, C.W.—"Effect of Diet on Growth and Eye-colour Development in *Drosophila*."

MELCHERS, G.—"Neuere Untersuchungen über die Physiologie der Genwirkungen an Pflanzen."

CHEVAIS, S.—"Contribution à l'étude du développement de l'œil du 'mutant' Bar de *Drosophila melanogaster*."

CARIDROIT, F.—"Phénomènes d'hérédité liée au sexe, d'hérédité contrôlée par l'hormone testiculaire et de 'Crossing-over' dans les croisements entre les races Sebright Doré et Sebright Argenté."

ANDERSON, R.L.—"Non-autonomous Development of Transplanted Eyes in *Habrobracon*."

9.15 a.m. THEME 4 SECTION D

NUTRITION AND GENETICS

Genetics Lecture Theatre. *Chairman:* J. F. DUNCAN.

WINTERS, L.M.—"Records of Performance for Meat Animals."

DUNLOP, G. and WILLIAMS, S.—"Controlled Feeding Techniques for Measuring Genetical Differences."

9.15 a.m. THEME 5 SECTION E

PLANT IMPROVEMENT

Chemistry Lecture Theatre No. 2. *Chairman:* A. MÜNTZING.

BANGHAM, W.N.—"Breeding of *Hevea*."

MANN, C.E.T.—"Improvement of Yield in *Hevea brasiliensis*."

STOUT, A.B.—"Hybridization and Selective Breeding in the Genus *Hemerocallis*."

WOODWORTH, C.M.—"Inhibiting Factors in Soy Beans."

SCHREIBER, F.—"The Genetics of Partial Coloration in Beans."

WEDNESDAY, 30 AUGUST (*continued*)

9.15 a.m. THEME 6 — SECTION F

HUMAN CHARACTERS

Engineering Lecture Theatre. *Chairman:* H. MADISSOON.

KEMP, T.—"The Human Chromosomes."
BURKS, B.S.—"Autosomal Linkage in Man."
WAARDENBURG, P.J.—"Concerning Dominant X-chromosomal Inherited Eye-defects in Man."
FELDMAN, W.M.—"The Inheritance of Congenital Transposition of the Viscera."
GARTH, T.R.—"A Review of Race Psychology."

9.15 a.m. THEME 7 — SECTION G

POLYPLOIDY AND REPRODUCTIVE MECHANISMS

Geology Lecture Theatre. *Chairman:* A. F. BLAKESLEE.

MÜNTZING, A.—"Incompatibility and Fertility in Experimental and Natural Polyploids."
CHRISTOFF, M.—"Polyploidy and Apomictic Development in the Genus *Potentilla*."
SMITH, S.G.—"Cytology and Parthenogenesis of *Diprion polytomum* Hartig."
SEARS, E.R., SMITH, L. and O'MARA, J.G.—"Genetic and Cytological Investigations of Polyploid Series in *Triticum* and Related Genera."
STOMPS, T.J.—"On Artificially Produced *Oenothera Lamarckiana gigas*."

10.30 a.m. THEME 2 — SECTION B

CYTOLOGICAL ANALYSIS

Zoology Lecture Theatre No. 2. *Chairman:* B. P. KAUFMANN.

FANKHAUSER, G.—"Polyploidy in Salamanders."
SAEZ, F.A.—"Efectos de la centrifugación sobre las células sexuales de *Schistocerca paranensis*."
MATTHEY, R.—"Le mythe des hétérochromosomes chez les Sauropsides."

2.15 p.m. THEME 1 — SECTION A

GENE MUTATION (*cont.*)

Zoology Lecture Theatre No. 1.

Chairman: P. W. WHITING.

RHOADES, M.M.—"On the High Mutation Rate of the a_1 Allele in Maize induced by the *Dt* Gene."
BURGEFF, H.—"Konstruktive Mutationen bei *Marchantia*."
CLEMENTE, L.S.—"The Lethal Effect of the Combined Purple and Eyeless Genes in *Drosophila*."
MA, SUNG-YÜN.—"Experimental Studies on the Induction of Heat Modifications in *Drosophila melanogaster*."
PLOUGH, H.H., CHILD, G.P. and IVES, P.T.—"The Importance of Temperature and Heredity for Mutation Frequency in *Drosophila*."

2.15 p.m. THEME 2 — SECTION B

CYTOLOGICAL ANALYSIS (*cont.*)

Zoology Lecture Theatre No. 2.

Chairman: O. ROSENBERG.

BERGNER, A.D.—"Chromosome Association in *Datura*."
LEVAN, A.—"The Occurrence in Nature of Asynapsis in *Allium amplectens*."
HUSKINS, C.L. and WILSON, G.B.—"The Structure of Chromosomes during Meiosis in *Trillium erectum* L."
BHADHURI, P.N.—"A Study of the Relation of Chromosomes to Nucleoli in Species of *Scilla*, *Vicia*, and *Oenothera*."
PATHAK, G.N.—"Studies in the Cytology of Crocus and Cereals, with Special Reference to Satellites and Nucleoli."
SIKKA, S.M.—"Cytological Investigations of *Brassica* Species and Hybrids."

2.15 p.m. THEME 3 — SECTION C

BIOCHEMICAL

Chemistry Lecture Theatre No. 1.

Chairman: M. R. VANDENDRIES.

PRICE, J.R.—"The Rate and Sequence of Gene-controlled Chemical Processes."
LAWRENCE, W.J.C.—"The Chemistry and Genetics of the Flower-colour Pigments in the Genus *Streptocarpus*."
MIEGE, E.—"L'hérédité de la composition chimique chez les hybrides intergénériques."

2.15 p.m. THEME 4 — SECTION D

PIG

Genetics Lecture Theatre.

Chairman: G. SCOTT ROBERTSON.

MCMEEKAN, C.P. and HAMMOND, J.—"The Relation of Environmental Conditions to Breeding and Selection for Commercial Types in Pigs."
DONALD, H.P.—"Genetic Aspects of Growth Rate of Bacon Pigs."
DAVIDSON, H.R.—"Practical Aspects of Improving Pigs."

2.15 p.m. THEME 5 — SECTION E

GENETIC ANALYSIS

Chemistry Lecture Theatre No. 2. *Chairman:* A. TAVČAR.

BOERGER, A.—"Angewandte Genetik als entscheidender Faktor für das Vordringen des Weizenbaues im subtropischen Osten Südamerikas."
RANGANATHA RAO, V.N.—"Hybridization between Two Hybrids."
HIORTH, G.—"Versuche mit kultivierten und natürlichen Formen von Arten der *amoena*-Gruppe von *Godetia*."
RAMIAH, K. and KADAM, B.S.—"Genic Symbolization in Rice."

2.15 p.m. THEME 6 — SECTION F

HUMAN CHARACTERS (*cont.*)

Engineering Lecture Theatre. *Chairman:* T. KEMP.

WAARDENBURG, P.J.—"Concerning Sex-linked Inheritance in Man."
QUELPRUD, T.—"Variability and Genetics of the Human External Ear."
RACE, R.R., TAYLOR, G.L. and VAUGHAN, J.M.—"A Genetic Investigation of Acholuric Jaundice."

2.15 p.m. THEME 7 — SECTION G

POLYPLOIDY AND REPRODUCTIVE MECHANISMS (*cont.*)

Geology Lecture Theatre. *Chairman:* L. BLARINGHEM.

SKALIŃSKA, M.—"The Origin of Polyploidy in *Aquilegia*."
WILLIAMS, R.D.—"Incompatibility Alleles in *Trifolium pratense* L.: their Frequency and Linkage Relationships."
JEFFREY, E.C.—"Apomixis in the Genus *Trillium*."
FLECKINGER, J.—"Caractères morphologiques et végétatifs, en relation avec la triploidie chez le Pommier et le Poirier."
TINNEY, F.W.—"Cytology of Apomictic Seed-development in *Poa pratensis* L."

GROUP MEETINGS

Discussion on the Teaching of Statistics in Relation to Genetics

A meeting was convened to discuss the Teaching of Statistics in relation to Genetics. The discussion was opened by C. D. Darlington with J. B. S. Haldane in the Chair.

At the conclusion of the discussion, the following resolutions were passed:

(1) That the teaching of statistics should be carried out in conjunction with the teaching of practical genetics.

(2) That elementary statistical methods, in particular, tests of significance and their validity, should be included in the ordinary mathematical courses given at secondary schools.

(3) That the General Committee of the Seventh International Congress of Genetics be requested to transmit copies of resolution (2) to any educational bodies which it considers may be able to assist in its fulfilment.

(4) That the genetical societies of countries represented at the Seventh International Congress of Genetics be requested to discuss the teaching of statistics in relation to genetics and to transmit their final resolutions to the next congress.

F. YATES

Discussion on Plant Breeding Methods

A meeting of plant geneticists was convened to facilitate a free discussion of plant-breeding methods in the light of genetics. A tentative programme had been prepared and various members had agreed to lead the discussions. Owing to the general circumstances only one meeting could be arranged. It was held on Thursday, 24 August, with E. W. Lindstrom in the Chair and about ninety members present. The main object of discussion was "Methods of selection in self-fertilized plants". J. Philp introduced the subject by raising the question whether, and if so, how, genetic studies could assist the plant breeder in accelerating or in rendering more efficient the work of the breeder. F. Yates outlined the application of the discriminant function to plant breeding practice and suggested that it should be put to the test in a breeding programme. A lively discussion followed in which the speakers were sharply divided. Some were satisfied that present-day methods, in which genetic analysis played only a small part, were as good as might be desired. Others contended that consideration of the genetic foundations of variation is now hardly sufficient; and that chance played too large a part in selection. To exemplify this contention, O. H. Frankel outlined the methods used in wheat breeding in New Zealand where a very large material could be utilized far more advantageously if the genetic foundations of the essential characters were at all known.

The discussion was useful in opening up the problem, but further meetings were required to achieve definite conclusions. It was felt that at a future congress a similar group might be formed which should be allotted sufficient time for extended discussions.

Subjects set down for discussion, which could not be dealt with at this congress, were as follows: Utilization of species crosses; induced polyploidy; mutations and structural changes in plant breeding; methods of breeding cross-fertilized plants; plant collections; organization of plant breeding.

O. H. FRANKEL

Mouse Genetics

As a result of a circular letter sent in the spring of 1939 from the Jackson Laboratory to biologists interested in mouse genetics, a Committee was chosen consisting of L. C. Dunn, G. D. Snell and F. A. E. Crew to prepare recommendations in regard to symbols for mouse genes.

On Thursday, 24 August, an open group meeting on the subject of rodent gene symbolism was convened at which Professor Hagedoorn presided. This meeting considered a set of nomenclature rules drawn up by the Committee and discussed details of the News Service. The recommendations of the meeting as regards nomenclature have been submitted to the committee.

The Director and Staff of the Roscoe B. Jackson Memorial Laboratory at Bar Harbor, Maine, U.S.A., had kindly offered facilities for the publication in mimeographed form of the Mouse Genetic News. This offer was gratefully accepted. It was suggested that a register of stocks and the various pure lines should be drawn up; this should end the confusion in the naming of pure lines used in various laboratories which has arisen during the last few years. Stock lists of all the laboratories concerned should be published from time to time. It was further suggested that notice should be given by a laboratory before any stocks are discontinued; it has happened several

times in the past that valuable material has been irretrievably lost, because every laboratory has relied on other places for its maintenance. The News Service should also arrange for exchange of stocks, and it is hoped that its activities may be extended to rabbits and other rodents. An appeal should be made to all laboratories concerned to collaborate wholeheartedly by promptly answering correspondence and sending information.

The meeting then discussed the establishment of centres, preferably in the U.S.A., for the maintenance and safe keeping of stocks, particularly of genes (pathological and otherwise) which are not purposely kept by the fancy. The continuity of genetical work depends on keeping our genes alive; genes which have died out are as irrevocably lost as extinct animal or plant species. It was urged that this matter should receive the immediate consideration of the News Service, and that an appeal should be made to the Carnegie and Rockefeller Foundations for financial assistance.

H. GRÜNEBERG

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PAPERS AND ABSTRACTS

1

ABDERHALDEN, E. und HERRE, W. ***Die Anwendung der Abwehrproteinase-Reaktion für Fragen der Vererbung***

Mannigfache Forschungen von Abderhalden haben die Erkenntnis gefestigt, dass der tierische Organismus die Eiweisskörper seiner Gewebe und Zellen nach eigenen ererbten Gesetzmässigkeiten aufbaut. Es gelang weiter der Nachweis, dass bei parenteraler Zufuhr fremder Eiweisskörper zu deren Abwehr Fermentsysteme ausgelöst werden, die ganz ausserordentlich spezifisch eingestellt sind. Die darauf begründete Abwehrproteinase-Reaktion (A.R.) befähigt feinste Unterschiede im Aufbau von Eiweissstoffen nachzuweisen.

Es lag nahe diesen Forschungsweg auch für Probleme der Vererbung nutzbar zu machen. Nachdem festgestellt war, dass Inzuchtstämme von Meerschweinen Besonderheiten in der Beschaffenheit ihrer Eiweisskörper besassen, wurden Bastarde von Mufflon und Hausschafen untersucht. Dabei war zunächst auffällig, dass die A.R. recht uneinheitlich ausfiel. Einige Tiere wiesen in der Beschaffenheit ihrer Proteine ausgesprochene Beziehungen zum Vater, andere solche zur Mutter auf, während noch andere eine intermediäre Stellung einnahmen. Der Schluss, dass trotzdem in der Feinstruktur der Proteine sich Vererbungserscheinungen auswirken wurde dadurch gestärkt, dass sich überraschender Weise Zusammenhänge zwischen phänotypischen Eigentümlichkeiten und dem Ausfall der A.R. nachweisen liessen. Das gleiche zeigte sich bei Versuchen mit Schweinen. Auch bei diesen liessen sich zunächst rassespezifischen Eiweisskörper feststellen und darüber hinaus gelang es auch einzelne Individuen durch eigentümliche Proteine zu kennzeichnen. Bei Geschwisterschaften aus Kreuzungen verschiedener Rassetiere war das Erscheinungsbild und der Ausfall der A.R. recht verschieden. Unter sich zeigten die Tiere wenig Übereinstimmung in den Eiweisskörpern, aber entsprechend ihrem Aussehen fiel die Reaktion positiv auch mit nicht verwandten Tieren der Rasse aus, welcher die Tiere phänotypisch ähnlich waren. Noch überraschender war die Tatsache, dass entsprechend Wandlungen im Erscheinungsbild von Bastarden auch Veränderungen in den Eiweissstoffen nachweisbar waren.

Es ist somit die Feststellung gelungen, dass auch die Feinstruktur der Eiweissstoffe durch Erbeinheiten beeinflusst wird, und dass Beziehungen zu Körpermerkmalen vorhanden sind. In welcher Weise die Bildung dieser spezifischen Eiweissstoffe durch die Gene kontrolliert wird, und wie sich die Tatsache der Wandlung der Proteine bei der Bildung von Körpermerkmalen auswirkt, kann noch nicht übersehen werden. Die bisherigen Ergebnisse berechtigen aber zu der Hoffnung, dass es auf diesem Wege gelingen kann in die Zusammenhänge zwischen Gen und Merkmal tiefer einzudringen. Es erscheint weiter nicht ausgeschlossen, dass es mit Hilfe der A.R. möglich ist auch Tiere zu unterscheiden, welche äusserlich kaum Unterschiede zeigen, deren Anlagenbestand sich aber unterscheidet. Darüber sind weitere Forschungen im Gang.

2

ADDINGTON, L.H. and CUNNINGHAM, O.C.
An Inherited Di-mamilla in Milk Goats

Di-mamilla is an abnormality that has been observed in the experimental breeding herd of pure-bred and grade Toggenburg goats at the New Mexico Agricultural Experiment Station during the last decade, in a number of other herds of pure-bred and grade animals of various milking breeds, Toggenburg, Saanen, Alpine, and Nubian, and also in the herds of common short-haired goats of New Mexico, which were probably introduced to this region by the early Spanish explorers. The di-mamilla may have been introduced, though not necessarily, by the use of bucks of the Swiss milk breeds, since practically all of the herds of common goats that the authors have observed now show evidence of the introduction of some Swiss blood. Apparently the character is fairly widely distributed. In addition to being of some economic importance because it is troublesome in some cases when the doe is being milked, this character presents intriguing possibilities in genetic studies.

Two fairly distinct types of the di-mamillate condition have been observed. The first type has two orifices and appears to consist of two mamillae that have fused. The mamillary duct seems to be an enlarged or double duct which divides into two ducts leading to two openings before the end of the mamilla is reached. The second type has two mamillae that are joined at the base at the time the animal is born. As females mature, only one of the mamillae develops, the other forming a small protuberance on one side of the developed mamilla.

The di-mamilla observed in goats is quite distinct from that in the mamillae of the human and mare that frequently have two or more openings. Several of the di-mamillae in goats have been dissected at autopsy

and apparently the abnormality is in the mamilla only and does not involve the mammary gland. The condition may occur in both males and females, and either bilaterally or monolaterally.

The genetical analysis of 550 individuals suggests that: (1) Di-mamilla is an inherited abnormality in milk goats. (2) It is not inherited as a simple Mendelian recessive. (3) It is not inherited as a simple Mendelian dominant. (4) Two or more genes appear to be involved.

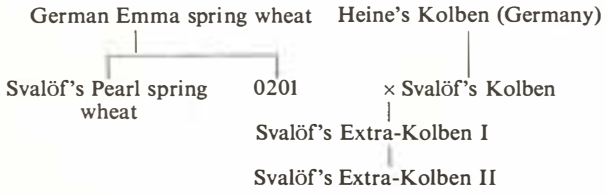
3

Åkerman, Å. *Spring-wheat Breeding in Sweden*

A survey of the progress of spring-wheat breeding in Sweden shewed that spring-wheat growing in this country began to acquire greater interest among the farmers comparatively recently. This is due to many conditions, first of all to the supply of an improved growing material.

The spring-wheat strains available at the beginning of the Swedish plant-breeding activities were early land wheats possessing a small grain, rich in protein, but they had also cardinal defects: low yield, weak straw, and susceptibility to yellow stripe rust. Foreign wheats tested proved to be more or less valuable but served chiefly as primary material for pedigree selection. In this way Svalöf's Kolben was bred from the German Heine's Kolben spring wheat. Another selection, Svalöf's Pearl, and a strain 0201, both originating from German Emma spring wheat, constituted a certain progress, but the grain yield was still too low for enabling spring wheat to compete successfully with barley and oats.

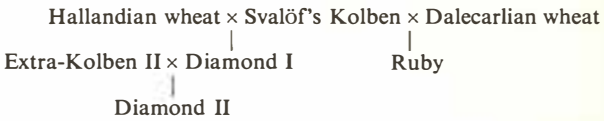
By the introduction of systematic cross-breeding new resources were available for spring-wheat breeding. The production of the Svalöf's Extra-Kolben wheats I and II is reported. Their pedigree was:



Svalöf's Extra-Kolben was in yielding capacity much superior to Svalöf's Kolben. After the production of Extra-Kolben II the chief problems of breeding in this cereal for southern Sweden have been to get strains with still higher grain yield and better quality. Concerning the quality, the results from baking tests (means of 7 years) at Svalöf with certain spring wheats were:

	Kolben	Extra-Kolben II	Land wheat from Holland	Diamond I
Crude protein content, %	13·1	11·7	13·1	13·6
Dough production from 100 g. of flour, g.	164	163	160	165
Specific volume of bread in c.c.	771	666	581	585

The search for earlier ripening spring wheats adapted to the interior and higher parts of the country —with about the same maturing time as the indigenous wheats—led to extensive pedigree selections in indigenous wheats, but this only resulted in the establishing of a greater uniformity in the investigated strains, the variation being very small (Nilsson-Ehle). Better success was achieved by cross-breeding. The pedigree of Svalöf's Ruby and Diamond spring wheats was:



The problem of combining the high specific yield of the later ripening spring wheats with the earlier maturing of the indigenous and other wheats was formerly looked upon with great scepticism. The progress of genetics, however, has fully proved the possibilities of this combination. Nilsson-Ehle thus has showed the possibility of such combination in both oats, winter and spring wheats.

The important problem of raising the quality properties of Diamond I (Åkerman) was solved by means of a backcross with Extra-Kolben II from which Diamond II was bred.

	Diamond I	Diamond II
Crude protein content, %	13·5	13·0
Dough production from 100 g. of flour, g.	165	165
Specific volume of bread in c.c.	611	690

Combinations between wheats of the Kolben type and certain very high-yielding west and middle European spring wheats (such as Brown Schlanstedter) are reported, and crosses between spring and winter wheats are discussed. In the latter combination experiments the segregation obtained is always very great, corresponding to the complicated interaction of the polymeric factors involved. Thus unexpected and undesirable characters often appear, e.g. suppression of resistance towards diseases, changes in stiffness of straw and other properties.

Finally, it is pointed out that Swedish spring-wheat breeding has not yet fulfilled all aims: the production of strains for different regions with 15–20 % higher yielding capacity than the Svalöf's Kolben, with very strong straw, proper time of maturing and the quality of the Fife wheat. The possibilities for further success along these lines are merely questions of size of breeding material and of precision and efficiency of methods.

4

ANDERSON, J. ***Artificial Insemination of Sheep and Cattle in Kenya***

Since 1935 several experiments on artificial insemination of sheep and cattle involving about 1000 cows and fully 5000 ewes have been carried out. Our technique is similar to that used by the Russians and by Walton, and it has proved quite satisfactory in practice.

It has been found that ram sperm can be diluted up to a maximum of ×8 without any reduction of fertility. It is highly important to get the majority of ewes in lamb as early as possible in the breeding season, for many non-pregnant ewes go for long periods before they return to the ram. Two inseminations in the one heat period, which have given better results than a single insemination, are therefore used. Although grade Merino ewes are capable of breeding throughout the year, it has been found that the oestrous cycle is shorter (about 17–18 days) from about December to March than at other times of the year, when it is considerably longer. The results from artificial insemination are better when the insemination is performed at a time of the year favourable to the reproductive processes in the ewe. The somewhat poorer results obtained from some experiments is probably to a large extent due to the inseminations having been performed at an unsuitable time of the year. Other points of importance which have been investigated are methods for determining the fertility of rams and insemination at different intervals in relation to the period of oestrus.

It is considered that the main problem in artificial insemination of cattle is the determination of the fertility of the bull from sperm examination. A combination of the available methods is used at present, but it seems that more attention should be paid to degrees of motility, and it is suggested that the survival period of sperm *in vitro* may perhaps provide a more reliable index of fertility.

Bull sperm undiluted and diluted up to a maximum of ×4 have given similar results. The majority of sperm specimens, when stored, retain a high degree of motility for 24 hr., and a smaller number for longer periods. Sperm stored for 24 hr. has given results very similar to that of fresh sperm.

The rapid extension of artificial insemination of cattle that has taken place in Kenya in the last two years is mainly due to the prevalence of genital disease which is transmitted by coitus. The practical application of artificial insemination to both cattle and sheep on European-owned farms is carried out by the farmers themselves who receive instruction in the technique at the Experimental Station, Naivasha. About 12,000 cows are now being inseminated per year in Kenya with satisfactory results, and with sheep results very nearly comparable with those from ordinary service have been obtained.

5

ANDERSON, R.L. ***Non-autonomous Development of Transplanted Eyes in*** **Habrobracon**

By the Ephrussi-Beadle technique for implanting eye disks into insects it is possible to check the eye development and pigmentation in the parasitic wasp, *Habrobracon juglandis*. Of the eye colours used (cantaloup *c*, orange *o*, ivory o^i, white *wh*, carrot wh^e, red *rd*, and wild type) only ivory and orange eye disks have so far exhibited non-autonomous colour development. Both ivory and orange eye disks are shifted toward wild type (dark red) when transplanted into the bodies of other hosts. When whole carrot and white eye disks are implanted into ivory-eyed hosts, the hosts' eyes are turned red. Small fragments of white or carrot and whole cantaloup, red or wild-type eye disks give rise to a brown coloration in ivory-eyed hosts. It is assumed that in *Habrobracon* the change in eye colour is due to a quantitative reaction in which the brownish coloration is only an incomplete stage toward the final red pigmentation.

6

ANDERVONT, H.B. ***The Use of Inbred Strains of Mice in Experimental Cancer***

Eight inbred strains of mice were studied to determine their relative susceptibilities to spontaneous, induced and transplantable tumours. The strains showed wide variations in susceptibility to all three types of malignancies. There was no correlation between the susceptibility to the induction of subcutaneous tumours by carcinogenic hydrocarbons and the susceptibility to spontaneous breast tumours, but there was a correlation between susceptibility to spontaneous pulmonary tumours and susceptibility to induced pulmonary growths. Those strains which develop

most spontaneous pulmonary tumours were most susceptible to induced lung tumours. This correlation in susceptibility to the two types of lung tumours may be due to the fact that the susceptibility to pulmonary tumours in mice is inherited according to genetic principles.

The strains also varied in their susceptibilities to the growth of transplantable tumours, but there was no correlation between the susceptibility to spontaneous or induced tumours and susceptibility to propagable growths.

Other outstanding characteristics of each strain were ascertained. These may be of interest to workers in genetics or experimental cancer. One strain develops spontaneous hepatoma, another develops lymphoma, and another develops an atypical stomach growth which is inherited as a recessive characteristic.

By the use of appropriate hybrid and backcross mice, it has been found that, in these strains, susceptibility to spontaneous pulmonary tumours, induced pulmonary tumours, induced subcutaneous tumours and transplantable tumours are inherited as a dominant characteristic.

The study yields information which should be of assistance in the selection of a suitable strain for experimental purposes.

7

ARMSTRONG, J.M., WHITE, W.J., MCLENNAN, H.A. and JOHNSON, L.P.V. ***Genetic Investigations in* Triticum-Agropyron *Hybrids***

The *Agropyron* species, *A. glaucum* and *A. elongatum*, may be readily crossed with tetraploid and hexaploid species of *Triticum*. The compatibility varies widely between species and between strains within species. Attempts to cross wheat with seventeen other species of *Agropyron* were unsuccessful. In the successful crosses tetraploid wheat gave plumper seed when crossed with *A. glaucum* than when crossed with *A. elongatum*. In the crosses with hexaploid wheat the condition is reversed, the plumper seed being obtained from the *A. elongatum* crosses. This endosperm condition affects the germinability of the seed.

F_1 plants from crosses involving *A. glaucum* are completely sterile (with a few exceptions), while in *A. elongatum* crosses a fair proportion of the F_1 plants shows low to moderate degrees of fertility. F_1 plants may be backcrossed to the wheat parents giving plants which are partially fertile. The seed setting is very low in the F_1 when the plants are grown in the greenhouse, but increases when the plants are grown under field conditions. This was shown to be due to increased anther dehiscence which in turn is affected by the percentages of good pollen.

Agropyron characters are dominant to a marked degree in the F_1 plants, this dominance being particularly pronounced in the *A. elongatum* crosses. The dominance relations for important characters are: *Agropyron* dominance in perenniality, vegetative vigour, and extent of mature root; partial *Agropyron* dominance in general morphological type, shattering of rachis, adherence of glumes to seeds and winter hardiness; intermediate inheritance in texture of mature root, size of seed, rigidity of leaf, and leaf pubescence.

The F_2 generation in three fertile crosses of *T. vulgare* × *A. elongatum* did not give the expected segregation of annual and perennial plants, about 95 % of the total population being perennial. This indicates a complex factorial condition for the character. In the second generation backcrosses approximately 25 % of the plants were perennial in habit.

A wide range of fertility was noted in the F_2 and backcross generations. In a random population of the cross, *T. vulgare* (C.A.N. 1835) × *A. elongatum*, 27·5 % were sterile while the mean fertility for the whole population was $6{\cdot}21 \pm 0{\cdot}39$ seeds per spike. In a second generation backcross (*T. durum* × *A. glaucum*) × *T. durum*, 34·6 % were sterile with a mean fertility for the population of $5{\cdot}88 \pm 0{\cdot}37$ seeds per spike.

The distribution of the F_2 population for leaf texture and spike characters was in general intermediate with some tendency for the distribution to be skewed in the *Agropyron* direction. This is contrary to the results from interspecific crosses in wheat where the number of intermediate types is low in comparison to types resembling the parents. These facts are related to cytological findings.

8

ASHOUR, A.M.M. ***The Use of Records in Estimating the Productive Ability of Dairy Cows***

The reliability of different systems of milk recording was examined in data from 267 normal lactations of Ayrshire cows in the herds of the Institute of Animal Genetics. For both milk and fat yield the differences between the maximum errors, the standard deviations and the limits of variation of the 21- and 28-day tests are insignificant, but it is concluded that for scientific purposes the test interval should not exceed 7 days. Data from 225 Ayrshire cows with five or more complete and normal lactations were used to assess the relative accuracy of individual records and combinations of records as indices of the producing ability of a cow. For both milk and fat yields the highest correlations existed between the

third and fourth, and second and third lactations. As the second and third lactations are highly correlated with the lifetime average yield, either of these would be, in the absence of further records, sufficiently reliable for the evaluation of a cow. The relatively low correlation between the first and the average lactation shows that, although the first record is widely used, it is nevertheless the least reliable. In progeny testing and selection the greatest importance should be attached to the highest and the third, and least to the first lactations.

9

ASTBURY, W.T. ***Protein and Virus Studies in Relation to the Problem of the Gene***

The problem of biological duplication seems for the moment to have resolved itself into that of the interaction of proteins and nucleic acids. The two simplest reproductive systems that we know—"simplest" in the sense of being nearest the beginning of things—are the viruses and the chromosomes. Most of the viruses so far isolated and examined in any detail are plant viruses, but they all appear to be nucleo-proteins; while the chromosome cycle is now recognized to be at least closely bound up with a protein-nucleic acid metabolism.

For molecular biologists the isolation by Stanley of the tobacco mosaic virus was undoubtedly the event of the century, and intensive studies by many workers, and in particular the X-ray findings of Bernal and his collaborators, have made it a prototype for discussions of this sort. Not all viruses are rod-shaped, but the tobacco mosaic virus is markedly so, and for this reason we naturally tend to think of it in closer relation to the chromosomes, especially in view of the suggestion that the rods found in highly purified preparations are not the true units themselves, but only linear aggregates of such units.

The tobacco mosaic rods are about 150A. thick and at least ten times as long. They have recently been made visible with the electron microscope, and each particle is sufficiently large and of such internal regularity of structure as to give rise to an X-ray single crystal pattern. This pattern persists even in dilute solutions: it is an *intra*-molecular pattern repeating along the rods at a distance of about 68A. Within this period, however, there is a kind of subunit of much smaller dimensions, possibly only $10 \times 10 \times 11$ A., according to Bernal's most recent suggestion. The smallest *chemical* subunit, based on a nucleic acid content of 5%, has a volume of $20 \times 20 \times 22$ A.: it is associated with one nucleotide and about fifty-four amino-acid residues.

Ultimately we have to find out the structure of the subunit, but just now it is important enough even to realize that there is such a thing: the virus molecule, like other giant proteins, is not made in one stroke, but by piecing together comparatively small fragments. These fragments are the raw material of the living cell. Anabolic and katabolic processes are going on continuously side by side, and the building of a protein may be under the control of structures external to itself, or it may be something inherent in itself. Probably there are both self-propagating proteins and proteins that have to be helped, so to speak. If it is true, as seems likely, that all enzymes are of a protein nature, we are driven to some such conclusion. At any rate, the virus molecule, a *nucleo*-protein be it emphasized once again, seems to be self-propagating in the correct physico-chemical environment; and, as far as we can see, one phase or aspect of its growth is *lengthways*. The X-ray data make that clear, just as they do in all fibrous protein molecules and so many other natural and synthetic high polymers and condensation products. The building stones are added in a row in a definite order. This does not mean that the virus molecule is necessarily a single chain—X-rays indicate that the complete unit in a natural protein fibre is at least a group of chains, and whether the length of the virus rod is constant or not, its thickness always amounts to 150A., a number of the same order as the large side-spacings given by other protein fibres. The width of a single polypeptide chain is about 10A., and its thickness about 4½A.

The virus unit, then, may duplicate itself either lengthways or sideways—we do not know. It is a fair conclusion that nucleic acid is essential to the process, and in fact to all processes of biological duplication; but we have no clear idea which way in the structure run either the protein chains or the nucleotides. The nucleic acid almost certainly pre-exists as such in the virus, and not as single isolated nucleotides, and on separation from the protein it gives an X-ray photograph like that of the polynucleotide from the pancreas. This nucleic acid is said to be a penta-nucleotide, and since it does not incorporate a desoxy-sugar, it is more closely related to yeast nucleic acid than to the thymonucleic acid of the chromosomes. Each nucleotide in the virus has in some way the power of co-ordinating about fifty-four amino-acid residues. Possibly there is a spiralized column of nucleotides about which the protein chains entwine themselves, and if this is so the concept of endless lengthways duplication at once becomes plausible. At any moment we may imagine some part of the nucleotide skeleton projecting from the end to form a kind of key-pin from which the protein entwinement continues ever anew. On the other hand, if we do not like this idea but prefer that of lateral duplication, perhaps we can make use of the other principal fact

revealed by X-rays—that the complete unit in a natural fibrous protein appears always to comprise a *group* of chains. It may be that this is the clue to the mechanism of lateral duplication. It is conceivable that in order to reproduce one chain exactly we have to pass through a succession of somewhat dissimilar chains before finally attaining the counterpart of that from which we started. And in this connexion we ought to bear in mind that only left-handed amino-acids appear in the end-product: this suggests that a given protein is constructed either from an *external* molecular "template", or it duplicates itself by somehow eliminating or overstepping intermediate enantiomorphous stages. In the latter case it is just a possibility that one of the functions of a column of nucleotides is that of bridging the enantiomorphous stage. As we shall see shortly, the spacing of successive nucleotides in a column is almost exactly equal to the spacing of successive side-chains in a fully extended polypeptide.

The chromosome is essentially a linear succession of *different* self-duplicating units. As Caspersson has shown, bands incorporating thymonucleic acid alternate with regions free from this acid. Such a structure at once invites comparison with that of the rod-like tobacco mosaic virus. The latter is a linear succession of similar subunits, and if we confine ourselves to the power of duplication only, it is not unreasonable to think of it as a row of identical genes. We need not attach too much significance to the fact that different types of nucleic acid are involved, since X-ray studies indicate that all the nucleic acids are stereochemically interrelated: nor are we yet justified in arguing too closely from the nucleic acid content in the two cases, because first, the virus is a single molecular entity while the chromosome is more of an "organism"; secondly, though the nucleic acid content of the salivary chromosomes is of a similar order (perhaps 10%), chemical analytical data on chromosomes are still almost negligible; and thirdly, there is no reason to assume that the amount of nucleic acid involved in the actual reproductive process is the same as that finally incorporated in the end-product. Caspersson has shown that the mitotic cycle synchronizes with a rise and fall of nucleic acid detectable by his ultraviolet absorption technique, but we have no method of telling how much nucleic acid is in combination at any moment. Caspersson's observation is nevertheless of the utmost significance in that it so clearly links up chromosome division with a nucleic acid metabolism.

If we ask ourselves the reason why with the proteins the nucleic acids are the chosen reactants in nuclear division, we have as yet no answer; but X-rays have brought to light a dimensional relation between the two that can hardly be accidental. Caspersson, Hammarsten and Signer have shown that the unit of sodium thymonucleate in solution is a rod-shaped body about 300 times as long as it is broad, and X-ray photographs of oriented solid preparations add precision to the picture by defining the rod as a column of flat nucleotides spaced at a distance apart of about 3·34A. This distance is almost exactly the spacing between successive side-chains in a fully extended polypeptide, and hence a thymonucleic acid column and a polypeptide chain should combine side to side with the greatest ease. This inference is confirmed by an X-ray and optical study of the fibrous compound formed by thymonucleic acid with the sperm protamine, clupein. Fibres of clupein thymonucleate are optically negative and show the same outstanding period of 3·34A. along the fibre axis. It is evident that a zipper-like combination takes place between the numerous basic side-chains of the clupein chain and the phosphoric acid groups along the thymonucleic acid column.

If such compounds as this artificial protein nucleate are present in the chromosomes, then it follows that in the latter not only the thymonucleic acid columns but also the protein chains run in the direction of their length; for optical studies such as those of Schmidt and Pfeiffer of the nucleic acid-containing bands of the salivary chromosomes show that they too are optically negative: the nucleotides are transverse to the chromosome length, and therefore the protein chains in combination with them must run *along* the chromosome length.

If we are looking for the molecular basis of the linear genic pattern along the chromosomes—and of course many of us are—here then is an experimental answer that is worth considering. The physico-chemical properties of the chromosomes, with their lateral swelling, their longitudinal splitting and their enormous capacity for altering their length, seem to be essentially fibre-like, and particularly protein fibre-like; but there was no stronger evidence than this that the protein chains do actually run along the chromosome length, as they should do. The new evidence is more convincing, and perhaps now for the first time we are justified in indulging an idea that at once springs to the mind—that a system of polypeptide chains, with their numerous and varied side-chains and their power of changing shape by intramolecular folding, would appear to be ideally suited to the task of bearing the patterns of life. We have long known that the proteins are the fundamental constituents of living things; perhaps they are fundamental in this deepest sense of all.

The picture of a chromosome conjured up by speculations of this sort is one of a kind of "carrier wave" of protein chains running from end to end, but "modulated" at intervals by columns of thymo-

nucleic acid running in the same direction. In the salivary chromosomes the bands so formed seem to be relatively rigid, while the interspaces remain quite extensible, as we might expect. The exact role played by the nucleic acid is unknown, but it is stimulating to think of it as exercising an intramolecular dimensional control at least for part of the time. May it not be that some stage in the mitotic cycle when the protein chains are fully extended is decided by the fact that the spacing between successive side-chains must then be equal to that between successive nucleotides?

In this picture it is not clear what proportion of the contractile power of chromosomes is to be ascribed to the intramolecular folding of individual polypeptide chains, but for future reference it should be noted that certain natural protein fibres show thermal contraction down to something like one-sixth, or even one-eighth, of their stereochemically fully extended length; while if we consider a corpuscular protein molecule of the 35,000 group (diameter about 40A.) to consist effectively of a single polypeptide chain, it could theoretically unfold to a length of about 1000A., that is, 25 times as long.

Probably, however, our present notions on chromosome structure are far too simple. We are sadly in need of a great deal more experimental data, and because of this our ideas are cramped. The proteins are tremendously important, but it is important too not to think too much in terms of proteins alone, or to endow the genes with self-sufficing properties: there must be many other accessory molecules—the nucleic acids are an outstanding example—and any intramolecular, or even interatomic, change could conceivably deflect the path of development—which, indeed, still proceeds a long way after the first cell division. It is undoubtedly true that some sort of protein chain system, in combination with other molecular groups, sounds quite the most attractive proposition at the moment, but it is the easiest thing in the world to think of objections. Our greatest difficulty still is that we have no really sound views on the mechanism of duplication, and the problem has been made no lighter by the X-ray discovery that fibrous proteins *with different chemical constitutions* can have similar molecular configurations. The implications of such a generalization, which probably also underlies the structure of the Svedberg groups of corpuscular proteins, is that configuration is decided not by constitution alone: some other factor must be invoked, something *external* to the protein under construction. What then is the gene? Is it a structure that is handed on, or is it a set of physico-chemical conditions? Certain things suggest the one, while other things suggest the other: it seems most likely that we cannot dispense with either.

Our best approach to the structural problem is now by way of the crystalline viruses, and especially the tobacco mosaic virus. It may be countered that the unit in other viruses, such as bushy stunt and vaccinia, is not elongated but round, so what of those? The answer to this is that it is hardly conceivable that molecular duplication is an affair of more than two dimensions, and in any case the present verdict of X-rays and biochemistry is overwhelmingly in favour of the view that all proteins are stereochemically related and fundamentally of a fibrous nature; they are all manifestations of the folding and states of combination of polypeptide chains.

One feature already recognized in the structure of the tobacco mosaic virus commands our immediate attention, that it is built by the exact, or approximate, repetition of relatively small subunits. It is a sound working hypothesis that these subunits correspond to the minimum reproductive groups, and therefore, by analogy, to the smallest part of a chromosome that we may describe as a gene. Chemically we ought not to consider anything below the volume associated with a single nucleotide. In the tobacco mosaic virus this volume is about 8800A.[3]

10

AUERBACH, CHARLOTTE. ***Tests of Carcinogenic Substances in Respect of their Influence on Mutation in*** **Drosophila melanogaster**

On the somatic mutation theory of cancer it is assumed that carcinogenic agencies, such as X-rays or carcinogenic substances, can cause mutations in somatic cells. If this action were brought to bear on germ cells its effects would be detectable as mutations in the progeny. X-rays, besides inducing cancer, are already known to raise the mutation rate of germ cells. If now the same could be proved for carcinogenic substances, this would indicate that the coincidence of these two effects was not accidental and thus would lend considerable support to the mutation theory of cancer.

In an attempt to investigate this point various carcinogenic substances (1:2:5:6-dibenzanthracene, 9:10-dimethyl-1:2-benzanthracene, and methylcholanthrene) were introduced as crystals or by injection of colloidal solutions into the abdomen of *Drosophila* larvae and young male and female imagoes. Controls from the same stocks were injected with similar solutions, only carcinogenic substances being omitted. Experimental flies as well as controls were kept under different conditions of temperature and food, and their progeny produced during the period from 7 to 14 up to 50 days after injection was tested for sex-linked lethal mutations.

The total number of tested chromosomes was 7769 in the experimental groups, and 3523 in the controls.

None of the substances and techniques used gave a detectable increase in mutation rate over controls. Though the amounts of substances introduced were very small (0·2 on the average) when considered in relation to the body weight of the average fly, they were comparable with 40 mg. for a rat of 200 g. body weight. This dose is more than sufficient for tumour induction in rats with any of the substances used. The lack of a detectable effect on mutation thus cannot be ascribed to insufficient substances, although it might conceivably be attributed to differences in time allowed for action, in penetration to tissues, or in metabolic processes.

11

BAGG, H.J. ***The Selection of Genetic Material for the Study of the Inheritance of Mammary Tumours in Mice and Rats***

Forced breeding of young females, either mice or rats, coupled with the prevention of suckling of the young, has made it possible to determine at a relatively early age those individuals whose constitution is either favourable or unfavourable to the formation of mammary gland tumours. The value and method of use of this procedure in the selection of genetic material is indicated.

12

BALTZER, F. ***Ueber die Rolle des Kerns in der Embryonalentwicklung: Typen der Letalität und Austauschbarkeit artverschiedener Kerne bei Bastarden***

Das Experiment der Bastardmerogonie besteht darin, dass einer Eizelle vor oder kurz nach der Befruchtung der arteigene Kern weggenommen und das entkernte Plasma durch Bastardbefruchtung mit dem Kern einer fremden Art versehen wird. Bei solchen haploiden Bastardkeimen stellen sich wichtige Probleme der genetischen Entwicklungsphysiologie. Insbesondere stellen die Merogonieversuche an Amphibienbastarden und die Entwicklung bastardmerogonischer Transplantate und Chimären, die wir in Bern seit Jahren ausgeführt haben und von denen ich hier sprechen möchte, zwei Hauptfragen:

(1) Ist ein Kern einer bestimmten Art (z.B. *c*, *Triton cristatus*) mit dem Plasma einer zweiten Art (z.B. *p*, *Triton palmatus*) imstande, normale Entwicklungsarbeit und Organdifferenzierung zu leisten? Und in welchem Grade ist das bastardmerogonische System zu solcher vitaler Entwicklung fähig? Gilt sie gleichmässig für alle Keimbereiche, die aus bestimmten Plasmabereichen des Eies hervorgehen; gilt sie gleichmässig für alle aus ihnen entstehenden Organe?

(2) Wenn solche artfremde Kern-Plasma-Systeme sich nicht vital entwickeln, sondern letal sind, gibt es dann verschiedene Typen von Letalitäten? Beide Fragen berühren das Grundproblem, in welchem Grade Erbfaktoren—gegeben im Plasma-fremden Kern—und Plasmafaktoren—gegeben in den verschiedenen prospektiven Bereichen des Eies—an embryonalen Entwicklungsprozessen beteiligt sind. Bei der Diskussion dieses Problems für die Merogonieversuche an Amphibien haben wir naturgemäss, da es sich in hohem Grade um ein Letalitätsproblem handelt, die Ergebnisse der Rassenletalität mit zu betrachten. Diese sind von genetischer Seite gut bekannt, man kennt die einzelnen Letalfaktoren. Aber sie sind nur in geringem Mass von entwicklungsphysiologischer Seite her bearbeitet worden. Im Gegensatz dazu ist die genetische Kenntnis der merogonischen Amphibienbastarde durchaus mangelhaft. Es ist bei ihnen genetisch nur der eine komplexe Ausgangspunkt gegeben: ein artfremdes Gesamtgenom, über dessen Abweichungen vom arteigenen Genom im einzelnen wir nichts wissen. Dagegen sind diese Amphibienbastarde entwicklungsphysiologisch sehr gut bekannt. Es standen uns hier von Anfang an die Ergebnisse der Schulen von Spemann, Harrison, Vogt, Woerdeman und anderer Forscher zu Verfügung. Dazu fügte sich die Aufklärung, die durch die entwicklungsgeschichtliche Analyse der merogonischen Bastardkeime selbst (der Ganzkeime) und durch die Verwendung von Transplantation, Chimärenbildung und Explanation gegeben wurde. Es sind Experimente, die vom Sprechenden begonnen (Baltzer, 1930) und dann vor allem von Hadorn (1930–7) weiter entwickelt wurden.

In der hier zu gebenden allgemeinen Uebersicht sind drei Fragen besonders hervorzuheben:

(1) Gibt es bestimmte Typen der letalen Entwicklung und entsprechen sie bestimmten Bastardkonstitutionen?

(2) Tritt die Letalität in bestimmten Entwicklungsstadien ein?

(3) Erfasst sie bestimmte Keimbereiche und Organanlagen oder ist die Letalität gleichmässig über alle Gewebe verbreitet?

(4) Gibt est Kombinationen ohne Letalität, sei es der ganzen merogonischen Bastarde oder (bei Transplantaten auf normale Wirte) einzelner Embryonalbezirke oder Organanlagen?

Wir wollen diese Fragen an Hand verschiedener Beispiele betrachten.

Fall 1. *Die Letalität ist in hohem Grade auf einen bestimmten Keim- oder Organbereich beschränkt und*

äussert sich in einer begrenzten Entwicklungsperiode. Dieser Fall ist gegeben beim bastardmerogonischen Kopfmesoderm der Kombination (*p*)*c*=*palmatus*-Plasma+*cristatus*-Kern. Die Gastrulation kann, noch annähernd normal vor sich gehen. Das Kopfmesoderm aber degeneriert unter Kernpyknose nach Schluss der Neuralwülste. Nahe benachbarte Organe, wie die Epidermis, der Vorderdarm und vor allem die Chorda, bleiben gesund. Dieser Letalitätstypus ist am ehesten zu vergleichen der Genletalität bei der Stummel-Maus; auch bei ihr degeneriert ein *bestimmter Bereich*; es ist in diesem Fall der hintere Rumpfbereich. Und auch hier trifft die Letalität eine bestimmte Entwicklungsperiode, es ist der 8./9. uterine Entwicklungstag (Chesley, 1935).

Fall 2. Die Letalität ist nicht als lokalisierte Gewebspyknose nachweisbar. Sie ist "diffus", d.h. sie scheint den ganzen Keim zu erfassen und ist morphologisch viel weniger deutlich. Dieser Fall liegt vor bei der Kombination (*a*)*p, alpestris*-Plasma +*palmatus*-Kern (Baltzer und de Roche, 1936, de Roche 1937). Auch hier gibt es ein *entscheidendes letales Stadium*: es ist wiederum der junge Embryo nach der Neurolation. Möglicherweise ist dieser Fall in seinem allgemeinen Typus vergleichbar der allgemeinen Hemmung des Krüperhuhnembryos am 4. Befruchtungstag nach Landauer und David.

Fall 3 *und* 4. Die Letalität trifft schon ein Stadium vor der Organentwicklung. Dies ist der Fall bei den Gattungsbastarden zwischen *Triton palmatus* und *Salamandra maculosa*. Bei dem Gattungsmerogon dieser Zusammensetzung, (*p*)*m*=*palmatus-Plasma*+*Salamandra maculosa*-Kern gehen schon während der späteren Furchung erhebliche Mengen von Chromatin verloren. Die Keime kamen niemals zur Gastrulation (Boehringer, 1938). Von Interesse sind hier die grossen Chromatinverluste; sie legen den Vergleich mit letalen Deficiencies bei *Drosophila* nahe.

Im diploiden Fall der gleichen Kombination: *pm*=*palmatus*-Plasma+Eikern+*maculosa*-Spermakern verläuft die Entwicklung zwar normaler, aber im Prinzip doch ähnlich letal. Auch hier beginnt die Anomalie (wie Schönmann (1938) gezeigt hat) schon während der Furchung; erstes sichtbares Zeichen sind abnormale Mitosen mit Chromosomennachzüglern in 22-stündigen Blastulen. In späteren Blastulastadien nimmt diese Mitosenerkrankung wiederum ab. Dagegen treten Kernpyknosen auf, die 30–50 % aller Zellen erfassen. Die Blastulahöhle der Keime füllt sich mit degenerierendem Zellmaterial. Die Keime beginnen meistens noch die Gastrulation, können sie aber nicht vollenden und sterben als unfertige Gastrulen ab. Zusammenfassend kann über diesen von Schönmann (1938) genau untersuchten diploiden Gattungsbastard folgendes gesagt werden: die Erkrankung beginnt hier besonders deutlich auf einem bestimmten Entwicklungsstadium und zwar wie im entsprechenden Merogon relativ früh: schon in der Blastula. Sie erfasst alle Keimbereiche, die animalen wie die vegetativen in gleicher Stärke, ist aber nur partiell letal insofern, als nur ein Teil der Zellen zugrunde geht, während die andern durch die Krankheit "hindurchschlüpfen" und normal bleiben Transplantate von solchem Restmaterial entwickeln sich normal (Lüthi, 1938). Für den Keim als *Ganzes* aber ist die Erkrankung völlig letal. Er kann trotz des Restbestandes an gesunden Zellen die anspruchtsvollere Phase der Gastrulation nicht überwinden. Aus dem Verlauf der ganzen Anomalie geht hervor, dass die primären Erkrankungsursachen schon in die Blastula fallen, und der Stillstand während der Gastrulation eine sekundäre Folge ist. Als Parallelfall für eine Erkrankung auf frühem Furchungsstadium bei letalen mendelnden Rassen sei die gelben Mäuse von Cuénot hingewiesen, die—ebenfalls in einer bestimmten Entwicklungsphase—als junge Blastula zugrunde gehen (Kirkham, 1919).

Haben wir bisher das letale Verhalten von Bastard-Ganzkeimen betrachtet, so wollen wir uns nun der Entwicklungsfähigkeit von Transplantaten und Chimären zuwenden. Die Transplantationsmethode hat sich seit 1926 (Baltzer, 1930; dann insbesondere Hadorn, 1930–7) also wertvolle analytische Methode für die Analyse der Letalität ausgewiesen. Sie hat es ermöglicht, das Problem der Letalität nicht nur für den Keim als Ganzes, sondern für seine verschiedenen Bereiche und Organanlagen zu stellen. Insbesondere haben die Transplantationen der Untersuchung der folgenden drei Fragen gedient:

(*a*) *Primäre Letalität.* Ist die Letalität eines gegebenen Keimbereiches oder Gewebes oder einer bestimmten Organanlage autonom? D.h. stellt sie sich auf dem Wege der Selbstdetermination ein? Untersuchungen dieser Art berühren sich mit denjenigen von Beadle und Ephrussi (1935–9).

(*b*) *Sekundäre Letalität.* Ist im Gegensatz zu dem eben erwähnten Fall die Letalität nicht autonom, sondern sekundär? D.h.: enthält das absterbende Gewebe in sich selbst keine letalen Faktoren und degeneriert es nur deshalb, weil ihm die notwendigen Antriebe zur Entwicklung von anderen benachbarten letalen Gewebe fehlen? Diese Möglichkeit berührt sich mit den von der Spemannschen Schule ausgearbeiteten Vorgängen der Induktion und Organisation (Spemann, 1936).

(*c*) In welchem Mass haben überhaupt einzelne Gewebe oder Organanlagen von Bastardkombinationen, die als Ganzkeime frühletal sind (wie (*p*)*c* und *pm*) *normale Entwicklungsfähigkeit*?

Fall 5. *Primäre, autonome Letalität des Kopfmesoderms bei* (*p*)*c.* Dieses Gewebe degeneriert mit Kern-

pyknose kurz nach Schluss der Neuralrinne zum Rohr. Die Letalität tritt nicht nur im merogonischen Ganzkeim, sondern—und zwar im gleichen Entwicklungsstadium—in ortsgemässen Transplantaten ein, die sich in einem *normalen* gleichaltrigen Keim entwickeln.

Fall 6. *Sekundäre, nicht-autonome Letalität des Ektoderms bei der Entwicklung von (p)c = Haftfäden und Kiemen.* Die beiden genannten Organe bestehen aus Ektoderm und Mesoderm. Die Beteiligung der beiden Schichten ist verschieden gross; die Kiemen haben einen umfangreichen, die Haftfäden einen geringen mesodermalen Anteil. In beiden Fällen aber werden die Leistungen des Ektoderms erst durch eine Induktion vom unterlagernden Gewebe her in Gang gesetzt.

In Längschimären (Hadorn, 1937), daran eine Hälfte in allen Schichten aus (*p*)*c*-Material besteht, entstehen auf der merogonischen Seite weder Haftfäden noch Kiemen, obgleich der Keim als Ganzes das entscheidende Entwicklungsstadium weit überschreitet und diese Organe auf der Wirtsseite entwickelt hat. Nach diesem Resultat könnte das Ektoderm primär letal, d.h. zur Bildung von Kiemen- und Haftfäden-Epidermis unfähig sein. *Ektoderm*chimären zeigen jedoch, dass die Epidermis dieser Organe nur sekundär von der Letalität der unterlagernden Gewebe betroffen wird. Bei diesen Ektodermchimären wird die merogonische (*p*)*c* Epidermis von normalem Mesoderm und Darm unterlagert. Hier bilden sich normale Haftfäden und normale Kiemen. Diese Epidermis ist also trotz der merogonischen Zusammensetzung für diese Organbildungen vital.

Wir haben bei den bisher besprochenen Fällen zwei Hauptkategorien von letaler Entwicklung vor uns, in denen das bastardmerogonische Zellmaterial aus ihm eigenen oder nicht eigenen Ursachen seine Entwicklungsunfähigkeit erwies. Ihnen sind die vital merogonischen Organbildungen gegenüber zu stellen. Ich wähle die zwei besten Beispiele aus: *die normale Entwicklung merogonischer Herzen und Chorden.*

Fall 7 *und* 8. Merogonische Transplantate und Chimärenhälften der Kombinationen (*p*)*c* und (*a*)*p* bilden schlagende Herzen und normale Chorden mit Vakuolisierung und Chordascheide[(*p*)*c* Hadorn, 1937; (*a*)*p* de Roche, 1937]. Hier durchläuft also das bastardmerogonische Gewebe, von anderen erkrankenden Geweben befreit, die normale Organgestaltung und eine normale Histogenese.

Diese ausserordentlichen Leistungen müssen wahrscheinlich dahin gedeutet werden, *dass der artfremde Kern in diesen Organbezirken zusammen mit dem ihm fremden Plasma die gleiche Entwicklungsarbeit leisten kann wie der arteigene Kern.* D.h. die Kerne der verwandten *Tritonarten palmatus, cristatus, alpestris* können sich, wenn auch nur *bei bestimmten Organentwicklungen* und den dabei sich stellenden Entwicklungsforderungen entwicklungsphysiologisch weitgehend vertreten.

Gegenüber dieser Schlussfolgerung können Einwendungen gemacht werden, die ich hier kurz zusammenfassen möchte. Die Vitalität könnte, statt autonom zu sein, auf anderen Ursachen beruhen: (1) auf einer Hilfe durch den Wirt; (2) auf mütterlicher Vererbung; (3) auf plasmatischer Vererbung.

(1) *Der Einwand der Hilfe durch den Wirt.* Obgleich bei manchen merogonischen Organentwicklungen eine Förderung durch das benachbarte Wirtsgewebe wahrscheinlich ist (so beim Neuralrohr), ist ein solcher Einfluss gerade bei der Herz- und der Chordaentwicklung sehr wenig wahrscheinlich. Einerseits entwickeln sich beide Organe überhaupt unter Selbstdifferenzierung, sind also in ihrer Entwicklung hochgradig unabhängig von den Nachbarbereichen. Zweitens, entwickeln sie sich auch dann normal, wenn sie in der entscheidenden frühen Periode noch allseitig von merogonischen Geweben umgeben sind, also direkte Kontaktwirkungen der Wirtsgewebe gar nicht in Frage kommen. Drittens, zeigt sich auch kein topographischer Ausbildungsgradient, der vor allem bei der langgestreckten Chorda zu erwarten wäre. Die merogonische Chorda ist in den Bereichen, die weit entfernt von dem normalen Wirtsgewebe liegen, ebenso gut entwickelt wie in den näher gelegenen Bezirken.

(2) *Der Einwand der Prädetermination* (mütterliche Vererbung). Nach dieser Erklärung würden sich merogonische Chorden und Herzen deshalb normal entwickeln, weil sich das Ei und die in ihm enthaltenen präsumptiven Chorda- und Herzbezirke im Ovar einer normalen Mutter entwickelten, und weil das Plasma von dort her eine normale Entwicklungsfähigkeit mitgebracht hätte. Gegenüber diesem an sich sehr interessanten Einwand ist darauf hinzuweisen, dass bei der Entwicklung der merogonischen Herzen wie der merogonischen Chorden jeder *zeitliche* Gradient fehlt. Während bei anderen Fällen von Prädetermination der mütterliche Einfluss im Lauf der Entwicklung abklingt (vergl. Plagge, 1938), müsste für die beiden merogonischen Organe ein *konstanter dauernder* mütterlicher Einfluss im Sinne der Vitalität angenommen werden. Dies ist um so unwahrscheinlicher, als beide Organe eine ganze Reihe von Entwicklungsschritten (der Organgestaltung und der Histogenese) durchlaufen müssen, also für das Abklingen des mütterlichen Einflusses die günstigsten Bedingungen bestünden.

(3) *Der Einwand der plasmatischen Vererbung.* In diesem Falle ginge die wesentliche Leistung in der Entwicklung der genannten bastardmerogonischen Organe vom Plasma aus und der artfremde Kern

wäre nur als Mitläufer zu bezeichnen, der wohl bei den Mitosen, nicht aber bei der eigentlichen Embryogenese mitarbeiten würde.

Nach allen bisherigen Erfahrungen ist jedoch die Leistung des Kerns wesentlich grösser. Dies wird durch die Feststellungen Fankhausers erneut betont, wonach gerade bei *Triton* Keimbereiche mit Zentrosomen und Sphären, aber ohne Kern nicht über die Gastrulation hinaus kommen. Ausserdem ist eine entscheidende Kernleistung gerade in frühen Stadien von Urodelenbastarden durch die Tatsache bewiesen, dass in Farbbastarden von Axolotl (weiss ♀× schwarz ♂) die speziellen Kernleistungen bei der Pigmentierung schon in jungen Stadien beginnen, über die die merogonischen Herzen und Chorden wesentlich hinausgehen. Es ist also nicht wahrscheinlich, dass bei diesen Organbildungen nur plasmatische und keine wesentlichen Kernleistungen beansprucht werden.

Der allgemeine Schluss, der aus der Tatsache der vitalen merogonischen Bastardorgane der Herzen und Chorden wahrscheinlich wird, muss nach diesen Erörterungen der folgende sein: wenn der artfremde Kern, ohne durch einen arteigenen Kern unterstützt zu werden, *bei der Entwicklung bestimmter Organe* die gleiche Arbeit leisten kann wie der arteigene Kern, so müssen sich die *Genome* der beiden Arten, *so weit sie für diese Entwicklungsprozesse gebraucht werden*, vertreten können. Einen wie grossen Teil des Genoms dies betrifft, wissen wir nicht. Denkbar ist, dass gerade die vitalen merogonischen Organe an den Kern verhältnismässig geringe Ansprüche stellen. Nach dieser Deutung wird die Entwicklungsfähigkeit der vitalen merogonischen Organe (wie der Chorda und des Herzens) durch die Homologie der für sie nötigen Teile des Genoms bedingt; die Letalität anderer Organe des gleichen Keimes (wie des Kopfmesoderms) wird durch die Gegensätzlichkeit der hierbei nötigen Teile des Genoms verursacht.

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13

BAMBER, RUTH C. *A Time Factor in White-spotting in Domestic Cats*

White-spotting in cats shows a graded series from self-colour to almost white. Self-white may also belong to the series. According to some workers the grades of spotting depend upon a series of multiple allelomorphs; according to others one pair of allelomorphs only is involved, the gradation depending upon variation especially in the heterozygote. Our own unpublished data suggest a series of allelomorphs (Bamber and Herdman).

The pattern of this spotting is fairly consistent in each grade and seems to show a connexion between the degree of white-spotting and the time in development at which the causal factor becomes effective.

The least amount of white found always occurs on the ventral side of the neck. When slightly more is present it is found also on the tips of the feet or in the axillae or the groins, or in any combination of these regions. A greater degree involves also the mid-ventral line, and the badge under the neck extends up the sides. In increasing degrees there is a spreading of the white areas up the legs and up the sides of the body and around the neck. In a high degree of spotting the only colour is found on the dorsal or dorso-lateral regions and on the tail. In the highest degree observed the only pigment present was in a tiny spot on the back of the head.

When such a series is examined in conjunction with a series of embryos showing successive stages of hair distribution it is found that in the lowest grades of white-spotting the white areas are those in which the hair appears last during development of the embryo: and in the highest grades the only pigmented regions are those in which the hair first appears. A series of embryos from older, almost fully haired, to younger, naked ones, presents a series of naked areas corresponding almost exactly with an ascending series of white-spotting grades in both degree and pattern.

It is suggested, therefore, that in cats the amount of white-spotting and its pattern depend upon the time in development at which the white-spotting factor becomes effective, the greater degree depending upon early onset the lesser degree upon late onset. The series would then be genetically comparable to Goldschmidt's series of intersexes in *Drosophila*.

14

BAMBER, RUTH C. ***Brown Degeneration of the Adrenal Gland in Mice***

Some of the lack of harmony amongst the observations of different workers in regard to the incidence of "brown degeneration", its nature and its possible connexion with the occurrence of cancer in mice, may be the result of the accidental confusion of several separate phenomena. In Liverpool different workers, under my direction, have, for some years, been studying the adrenal of various mammals entirely apart from cancer research, and some of their findings seem to have a bearing on the question. In the mouse the reticular zone and the much-discussed X-zone are undoubtedly separate structures. In development the X-zone (or interlocking zone) is found to be that part of the foetal cortex which remains after the adult or permanent cortex has become differentiated from the peripheral region (Waring, 1935). The X-zone is more strongly eosinophil than adjacent tissues, its cell boundaries are indistinct, and it interlocks with the medulla. In the male it begins to degenerate at about 35 days after birth, degeneration being complete at about 56 days. In the female it shows no sign of degeneration at this time but degenerates, during pregnancy or, in virgin females, in late adult life. The degeneration in the male is by a process of nuclear shrinkage accompanied by disintegration of the cytoplasm. In the female the process may be similar or there may be also intense vacuolization, probably due to lipoids.

The reticular zone is a part of the permanent cortex. It arises from the inner border of the fasciculate zone. It is less eosinophil than the X-zone, its cell boundaries are very distinct and it never interlocks with the medulla. In material fixed in Bouin's fluid and stained with Ehrlich's haematoxylin and eosin the two zones are clearly recognizable. After degeneration of the X-zone the reticular zone is separated from the medulla by a connective tissue capsule.

The reticular zone also shows a process of degeneration by fatty vacuolization, but never disappears, being almost certainly renewed by inward growth of the cortex initiated at or near the periphery (Waring and Scott, 1937). The vacuolization of the reticular zone, in our material, is much more common in the left gland than in the right; also it shows a striking seasonal variation, being most prevalent in March (Scott, unpublished). There is also some evidence that different strains show different degrees of vacuolization.

The above-mentioned phenomena may well confuse the issue in any discussion of degeneration of the adrenal cortex.

The phenomena are not specific to the mouse. An X-zone ("interlocking" or "boundary" zone) has been demonstrated in the cat by Davies (1937), and in the rabbit by Roaf (1935), and by Joshua (unpublished). In the cat it degenerates a few months after birth. In the rabbit it persists throughout life. Vacuolization of the reticular zone has been studied in the cat by Davies (unpublished) and in the rabbit by Roaf (1935) and by Joshua (unpublished).

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15

BANGHAM, W.N. ***Breeding of*** **Hevea**

Progress in the adaption of a jungle crop, *Hevea brasiliensis*, to large-scale agricultural utilization is outlined. Particular attention is given to the improvement in yield to more than double that of the original population in the course of 20 years of breeding and selection.

Populations obtained by selection and by breeding are compared and the utilization of budded rubber to the extent of 724,829 acres in the Middle East is mentioned.

16

BARBER, H.N. ***The Origin and Behaviour of Diplochromosomes***

The meiotic nuclear divisions of *Fritillaria Meleagris* can be completely suppressed by high temperatures (30° C.). Heating at early diplotene causes the nucleus to lapse directly into the pollen-grain resting stage. A chromatid division takes place normally during this resting stage to give, at the metaphase of the pollen-grain division, diplochromosome bivalents consisting of 8 chromatids. The diplobivalents retain the chiasma structure of the meiotic bivalents, but two chromatids replace one. The proximally localized chiasmata of normal *F. Meleagris* therefore appear as proximally localized diplochiasmata at each of which two pairs of chromatids exchange partner. There has been no movement of chromatids relative to one another during a resting stage lasting over a week.

Each chromatid in a diplobivalent is coiled independently of the others. The coil is probably a simple mitotic coil, since the nucleolar constrictions are usually visible. There is no well-defined attraction in pairs, each arm consisting of four more or less parallel chromatids at full metaphase. Thus joint coiling of

the major spirals is probably a condition of the retention of the arrangement of chromatids in pairs at first metaphase of meiosis.

Each half diplobivalent has a single centromere to which are attached the four chromatids passing through it. Each centromere orientates separately, so that the centromere loop of each diplobivalent is usually transverse to the long axis of the spindle. It follows that the special property of co-orientation of the centromeres at meiosis must depend on the internal structure of the centromere, not on chiasma formation or other external conditions.

At anaphase two successive chromatid divisions take place in each centromere. The first, at the beginning of anaphase, separates the products of pachytene division; that is, in a diplobivalent with a single diplochiasma, the first division separates the pair of cross-over from the pair of non-cross-over chromatids. The second division during anaphase separates the chromatid products of the pollen-grain resting stage so that two tetraploid daughter nuclei with normal chromosomes are produced.

17

BARIGOZZI, C. ***Cytogenetical Analysis of Two Wild Populations of* Artemia salina *in Connexion with Polyploidism***

Artom has shown that there are wild populations of *Artemia salina* living in different salt pans, having the same chromosome number, but very different nuclear sizes.

Since it is not known how many individuals from each pan Artom examined, or whether he determined both chromosome number and nuclear area of every individual, it is possible that this remarkable variation was due to:

(1) Surrounding influences (that is, a partial phenotypical determination of the nuclear sizes).

(2) Mixture of individuals with different chromosomal sets. It is possible to consider diploid individuals as polyploids with exceptionally small cells, if both measurement of nuclei and counting of chromosomes are not made in the same individual. It is to be noted that diploid and polyploid individuals are actually living together in salt pans at Margherita di Savoia.

I therefore measured the nuclear area in epithelial gut cells of 100 Artemiae taken from the salt pans of Portorose Pirano Sicciole (Istria), which are known to be parthenogenetic and octoploid. From each individual I drew the outlines of ten entire nuclei of the gut epithelium taken from the fourth to the seventh segment by dissection, and without cutting. Measurements were made with the planimetre, and of these ten measurements the average was calculated.

Then I measured:

(1) The distance between the most anterior point of the middle eye and the most medial point of the interior margin of the uterus.

(2) The distance between the most projecting points of the lateral eyes.

The results of this first series of measurements are the following:

A. The majority of Artemiae had almost similar values to the measured area. There are also individuals with nuclear areas enormously greater or smaller than the average; these I call macro- and micro-pyrenics.

B. There is no correlation between somatic and nuclear sizes.

Then I cultivated some eggs collected in Portorose. I used Schreiber-Föyn solution after Gross at the concentration of 3·5 Bé. as culture medium, and *Clamydomonas* were used as food. The cultures were kept at the temperature of 18–20° Celsius with strong and uniform lighting. Food was always plentiful.

Development took place very homogeneously for the whole culture. Sexual maturity was reached nearly contemporaneously by all the animals.

I measured many hundred specimens and I was able to observe the following facts:

(1) Even in the material cultivated in artificial conditions nearly the same variation in nuclear size is present as was observed in the wild individuals. The majority ranges from 0·75 to 1·00 μ^2. The smallest measures 0·52 μ^2 and the greatest 2·02 μ^2.

(2) The calculated sizes of the body seem to differ very little, and without any correlation with the nuclear area of the epithelian cells.

(3) Strong differences in nuclear area were observed in individuals with identical chromosome number; even in a hexaploid strain the nuclear area is greater than in an octoploid.

(4) The chromosome number (168, corresponding to the octoploid condition) is very constant in this population; in thirty individuals there were only one hexaploid and one probable tetraploid (84 chromosomes).

Thus the variation of the nuclear values does not seem to be due to either the variation in the chromosome number, or to external agencies. It is possible then to formulate a third hypothesis: that the nuclear size (expressed as nuclear area) may be determined by internal factors, e.g. particular genes or increase of chromosome size, without increase of number. This genetic explanation of the phenomenon must be supported by the following proofs:

(1) By inheritance of the average of the nuclear area in subsequent generations of pure lines.

(2) By Mendelian behaviour in amphigonic strains with different nuclear areas, when crossed.

Experiment has shown that:

(1) The average of the areas in sisters is remarkably similar.

(2) The average of the mother is very nearly the average of the offspring, i.e. from a micropyrenic female micropyrenic offspring will be obtained.

(3) There is an individual variability.

(4) There is no correlation between nuclear area and size of the body.

18

BAUER, H. ***Röntgeninduktion von Chromosomenmutationen bei*** **Drosophila**

Es wird die Frage nach der dosisabhängigkeit des Auftretens röntgeninduzierter Chromosomenmutationen auf Grund der Ergebnisse zweier Methoden behandelt: Nach Untersuchung der Speicheldrusenchromosomen von F_1-Larven nach *P*-♂♂-Bestrahlung ergibt sich für das Auftreten mutierter Spermien eine Kurve, die zwischen einer Zwei- und einer Dreitreffer-Kurve verläuft. Brüche und Kontaktpunkte zeigen exponentielle Abhängigkeit.—Aus der Verschiebung des Geschlechtsverhältnisses in der F_1 nach Bestrahlung von X^{c2}-*P*-♂♂ ergibt sich für das ♀♀-Defizit eine Kurve, die als übersättigte Eintreffer-Kurve zu deuten ist. Sie beruht auf dem unterschiedlichen Auftreten von Zygotenletalität-bedingenden Chromosomenmutationen in X^{c2}- und *Y*-Spermien, bezw. der Elimination von zu Doppelringen mutierten X^{c2}-Chromosomen.—Der Vergleich der durch die beiden Methoden gewonnenen Ergebnisse führt zu dem Schluss, dass unilokale Einzelereignisse (Brüche), die durch einen Treffer ausgelöst werden, sich zu zweien oder mehreren Kombinieren, um die Verlagerungen zu ergeben. Die Bruchkombination ist örtlich begrenzt. Die Häufigkeit der Einzelereignisse (Brüche) ist mindestens 4mal so hoch wie die induzierter Letalfaktoren.

19

BEADLE, G.W. ***Genetic Control of the Production and Utilization of Hormones***

INTRODUCTION

More and more instances are becoming known in which specific gene substitutions influence metabolic processes in specific ways. The work of Scott-Moncrieff (1936) and others on the biochemistry of anthocyanins and related pigments in various genetic types of flower colour is a well-known example. The failure of oxidation of xanthophyll of the fat of certain genetic types of rabbits (Bernheim), the inability of alcaptonurics in man to oxidize homogentisic acid (Garrod, 1923 and others), the failure of phenylketonurics to convert phenylpyruvic acid (Penrose, 1935), and the incomplete transformation of uric acid in the Dalmation coach hound (Trimble and Keeler, 1938), are examples in which a specific step in a chain of reactions is blocked, presumably because the enzymatic catalysis of some one reaction is defective. The defect or deficiency in the enzyme system in each instance can be attributed to a change resulting from a single gene substitution.

Examples such as these lead many geneticists to think that all metabolic processes are more or less directly under the control of the genetic system, and to share the belief of Haldane (1937) when he says: "... the new branch of biochemistry which will, I believe, arise from genetics, will be concerned largely with the stages of synthesis of such molecules as chlorophyll and cyanin. And its final goal will be the explanation and control of the synthesis of genes."

It is the purpose of this paper to review certain aspects of the relations known to exist between genes and hormones. No fundamental significance attaches to this segregation of systems involving hormones from others; the distinction is merely one of convenience. There is no good reason to suppose that hormones, which are carried through the circulatory system or otherwise move from cell to cell, are in any important way different from other substances which are produced and used without passing cell boundaries, and which could, if we desired, be called "intracellular hormones". The substances of nuclear origin that must be supposed, from Hämmerling's (1935) work, to control the nature of cap differentiation in the single-celled alga, *Acetabularia*, might be considered the intracellular equivalents of the true hormones of multicellular plants and animals.

ORGANIZER PHENOMENA

The long-standing problem of the nature and cause of tissue and organ differentiation is beginning to be attacked through the study of organizer phenomena. The substances assumed to be responsible for embryonic induction, while not usually referred to as such, may be regarded as hormones of early development—the names applied to them have no real significance. From the fact that individual species show diversities in the end results of differentiation, it is difficult to escape the conclusion that both the production and reactions of organizers are controlled by genes. Unfortunately, the accidental circumstance that the classical animals of experimental embryology offer difficult material to the working geneticist has retarded a joint approach to this general problem. No insuperable difficulty is involved, however, and it

may be hoped that when increasing numbers of experimental embryologists become more genetically minded and when more geneticists become actively conscious of the fact that the organisms with which they work are the products of development and differentiation, our insight into the manner in which the genes work through the intermediation of embryonic organizers will be deepened.

Sex hormones

The hormone systems concerned with the development of sex characteristics in the higher animals have been studied extensively, but unfortunately the genetic differences between the sexes are usually not simple gene differences but, instead, involve many genes. The situations in some of the lower plants and animals, such as algae, fungi and Protozoa, are probably more susceptible to genetical and physiological analysis. The work of Moewus (1934) and of Kuhn, Moewus and Jerchel (1938) indicates that the reactions leading to conjugation in *Chlamydomonas*, in which sex is known to be genetically controlled, are set off in some way by a mixture of the *cis*- and *trans*-isomers of the dimethyl ester of crocetin, a carotenoid pigment the *cis*-isomer of which is photochemically transformed into the *trans*-isomer. This chemical control of sex activity is very specific and is related in a precise way to the genetically determined sex type of the organism. Whether or not we call the isomers of the dimethyl ester of crocetin hormones depends on our definition of a hormone. They are produced by single-celled organisms, and may diffuse into the medium and affect other organisms. Regardless of the terms we use, the facts are certainly of the greatest significance in understanding the chemical basis of sex reactions in these organisms. Unfortunately, there appear to be rather serious inconsistencies in the results of Moewus, and we therefore must await independent confirmation on certain points before building on the basis of this work.

Hormone systems of mammals

Partly because of the medical implications, the field of mammalian endocrinology has made rapid advances within recent years. With notable exceptions, the significance of hereditary factors in the development and control of endocrine systems has received relatively little attention. Smith and MacDowell (1930) have shown that a monogenic recessive type of dwarfness in the mouse involves a defect in the eosinophiles of the anterior pituitary, and that normal growth relations can be largely restored by implanting normal anterior pituitaries into genetically dwarf mice. The gene substitution involved appears to bring about a suppression of the anterior lobe cells that normally elaborate growth-promoting hormones.

The relative role of hereditary factors in defects of the thyroid gland in man is not entirely clear in the case of cretinism, a defect ameliorated by the administration of thyroxin, but Davenport's (1932) work would indicate the existence of an hereditary predisposition to endemic goitre. The axolotl, a genetic race of the salamander *Amblystoma*, normally does not metamorphose but can be induced to do so by administering thyroxin. This appears to be a clear case of gene control of the differentiation and development of thyroxin-producing tissues. The role of the hormone insulin is well known in the treatment of diabetes mellitus in man. In this disease, evidently some reaction leading to the formation of insulin is blocked. The administration of hormone serves as an artificial by-pass to this gene-controlled step in metabolism.

Plant hormones

Within a few years rapid progress has been made in the study of hormone systems in higher plants (cf. Went and Thimann, 1937). Van Overbeek, 1938 *a*, *b* has shown that "nana", a monogenic recessive dwarf type in maize, is characterized by the ability of its tissues to inactivate auxin, by oxidation, at an excessive rate as compared with the tissues of normal plants. This particular gene substitution evidently brings about a modification of the oxidation-reduction system of the plant. The "lazy" character of maize, which differs from the normal by a single gene, is to be attributed to a defect in the system concerned with geotropic response. This in turn, according to Van Overbeek and others, is brought about by an abnormal distribution of auxin. Wettstein and Pirschle (1938) find that the recessive mutant "defecta" in *Petunia* is differentiated from normal by a hormone-like substance affecting chlorophyll development, flower size, leaf shape and other characters. The substance concerned is capable of moving across a graft union. Stein (1939) has found more or less similar relations to exist in certain mutants in the tomato and in *Antirrhinum*. Melchers (1937) has investigated two genetic types in *Hyoscyamus*, an annual and a biennial form, differentiated by a single gene. The difference apparently involves a flower-forming hormone, and is related to the effect of the photoperiod on flower determination. This and further studies will undoubtedly go a long way toward clearing up many problems connected with the phenomenon of photoperiodism in flowering plants.

Hormones in insects

Although it was long thought by insect physiologists that hormones play little or no part in insect development and metabolism, recent work has shown

the importance of several substances of this nature. The ring gland (corpora allatum) was found by Hadorn (1937) to be concerned with puparium formation in *Drosophila*. The ring glands of lethal giant larvae were found to be defective in this respect presumably because of their inability to elaborate a specific hormone. The puparium-forming hormone has been obtained by Becker and Plagge (1939) in extracts from *Calliphora*.

Ephrussi, Khouvine and Chevais (1938) have reported that *Calliphora* pupae contain a substance that is capable of modifying the number of facets in the bar eye mutant of *Drosophila*. It is to be expected that further studies of the production and utilization of this substance will clear up a number of the interesting relations known to exist in the development of the bar eye character.

Gene-controlled hormone-like substances are known to be concerned with eye-colour development in the meal moth *Ephestia* (Caspari; Kühn, 1937; Plagge; and others), in the parasitic wasp *Habrobracon* (Whiting, 1932), and in the vinegar fly *Drosophila* (Sturtevant, 1932; Ephrussi and Beadle, 1937). In each of these insects, under appropriate conditions, the absence of a hormone results in a light eye colour as compared with the colour developed in the presence of the hormone. In *Ephestia*, the a^+ hormone is produced by tissues of the gonads, brain and eye (see reviews by Kühn (1932) and by Becker (1938)). In *Drosophila* both v^+ and cn^+ hormones are formed by Malpighian tube cells and by eye tissue, while cells of the fat-body form only v^+ hormone. In spite of the differences in their sources there is evidence that the a^+ hormone of *Ephestia* and the v^+ hormone of *Drosophila* are the same (Becker and Plagge, 1937). The o^+ hormone of *Habrobracon* seems to correspond to the cn^+ hormone of *Drosophila* (Beadle, Anderson and Maxwell, 1937). Studies of the chemical properties of the eye-colour hormones of *Ephestia* (Becker, 1937) and of *Drosophila* (Khouvine, Ephrussi and Chevais, 1938; Tatum and Beadle, 1938) confirm the biological evidence of their similarities. The hormones come out in the amino-acid fractions, but they are not simple amino-acids. Their molecular weights appear to be of the order of 500. The hormones of *Drosophila* are known to be used by the developing eye (Ephrussi and Chevais, 1938).

Eye pigments of insects have not been extensively studied, but some information is available about those of *Drosophila*. Schultz (1935) has reported certain facts and the work has been carried further by Cochrane (1937), who examined the histology of various eye-colour types in *D. pseudoobscura*, and by Mainx (1938), who has investigated the phenotypic results of combinations of various eye-colour mutants in *D. melanogaster* as well as the chemical characteristics of the eye pigments found in wild type and in various mutants. Fortunately, the key eye-colour types can be homologized in these two species. There is good evidence from histology, from phenotypic interactions, and from the chemical properties of the pigments that the wild-type eye contains two distinct components, one red and water-soluble, the other brown and insoluble in all ordinary reagents.

An attempt is made in this paper to develop a generalized scheme of eye-colour development for *Drosophila* into which as many as possible of the known facts can be fitted. This is shown in Fig. 1. It

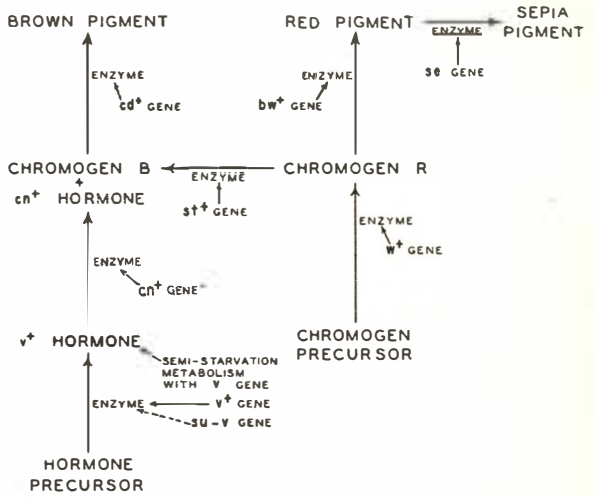

Fig. 1. Schematic representation of some of the processes assumed to be involved in the development of eye pigments in *Drosophila*.

is seen that v^+ and cn^+ hormones are indicated as being sequentially related, v^+ hormone in some way being necessary to the formation of cn^+ hormone. The evidence for this relation cannot be presented in detail here, but part of it has been summarized by Ephrussi (1938). This part of the scheme is consistent with many known facts. The formation of v^+ hormone is blocked in vermilion flies, and, as a working hypothesis, we may suppose this to be due to a defect in the enzyme system involved in the synthesis of the hormone. The precursors of this hormone are not known with certainty, but there is some reason for supposing that amino-acids, possibly tryptophane, may be concerned. It is interesting that, although the synthesis of v^+ hormone is blocked in vermilion flies, the production of this hormone can be partially restored in either of two ways. In a vermilion fly homozygous for the sex-linked recessive "suppressor-of-vermilion", v^+ hormone is produced. Furthermore, the metabolism of vermilion larvae can be altered, by subjecting them to a low food level, in such a way that they later produce v^+ hormone (Khouvine,

Ephrussi and Chevais, 1938; Beadle, Tatum and Clancy, 1938). The mechanism is not understood in either case, but there is evidence for supposing that the so-called starvation effect involves a shift in protein metabolism. The starvation effect can be inhibited by carbohydrates in the diet. If v^+ hormone is supplied to a vermilion fly, there is no further block in the system and the pigment develops normally. Administration of the hormone acts as a by-pass around the defective link in the chain of reactions in much the same way as does the administration of insulin to a diabetic.

A reaction leading to the formation of cn^+ hormone is interrupted by the substitution of cinnabar genes for their normal alleles. Again it is suggested that this block is brought about through a defect in the enzyme system catalysing a specific reaction. While, with the exception of the modification of the red pigment component in sepia flies (Mainx), there is no direct evidence for this intervention of enzymes in the system, they are assumed throughout for the reason that for the moment they appear to provide a simple mechanism by which genes might control reactions. Similar assumptions have, of course, been made by many workers, often with more justification. If one prefers, the enzymes can be omitted throughout the scheme.

A chromogen (*B*) is assumed to interact with cn^+ substance to give rise to the brown pigment component. Several alternative assumptions might be made at this point, and at present there appears to be no easy way of distinguishing which of them, if any, is correct. Since it is known that in both scarlet and cardinal flies the formation of the brown pigment component does not take place even in the presence of the v^+ and the cn^+ hormones, it may be supposed that either the st^+ or cd^+ is concerned with the reaction leading directly to the formation of brown pigment, and that the other is concerned with the production of the chromogen of the brown pigment. These two genes might be reversed in the scheme since their positions are assigned arbitrarily.

The red pigment component is assumed to be produced by a reaction involving a second chromogen (*R*). This reaction may be blocked by substituting the brown gene for its normal alleles. The two chromogens are assumed to have a common precursor from the fact that a modification of the wild-type allele of the white gene ($w^+ \rightarrow w$) results in the blocking of all pigment formation. While the relation shown, a sequential formation of chromogens *R* and *B*, has advantages of simplicity, alternatives are of course possible. Other genes, known from the work of Mainx to bring about a change in both pigment components, may be assumed to be involved in reactions leading to the first of the two chromogens (*R*).

Mainx has found that the red pigment component is qualitatively modified in sepia flies, but that the brown component is unaffected. This is indicated in the diagram as a reaction controlled by the sepia gene.

The interpretation presented is consistent with the key interaction effects of various eye-colour mutants. Thus, according to this scheme, the vermilion, cinnabar, scarlet and cardinal mutants should have identical end-results in spite of the assumption that each is characterized by an interruption of a different one of a series of related reactions. While there appear to be slight quantitative differences among these characters, they are phenotypically very similar. A combination of any one of the four recessives with brown gives a colourless or nearly colourless eye, a fact with which the scheme is consistent.

While the interpretation offered is based to a rather large extent on speculation, there is enough factual evidence in support of it to make it probable that the principle on which it is based, namely, a system of reactions occurring in series and in parallel, each of which is gene-controlled, is essentially correct.

In conclusion, it may be suggested that, if the work on genetic control of specific reactions outlined above is of importance, it is so not because it tells us much specifically about what genes do, but rather because it may indicate a method of attack which we may hope will become increasingly useful to both geneticists and biochemists. Progress in this general field—the relation of genetics to development and function which has been called physiological genetics, is dependent on a further breakdown of those artificial barriers that separate biology and chemistry. The migration across this barrier need not be unidirectional; there are many ways in which genetics can aid biochemistry and perhaps even more ways in which the geneticist can profit from co-operation with the biochemist.

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20

BELL, G.D.H. ***Cereal Breeding and Research at the Cambridge University Plant Breeding Station***

The methods and scope of improvement of the cereals cultivated in England are intimately connected with the climatic conditions, the economic and agricultural factors, and the comparative freedom from serious disease epidemics. The lack of any contrasting extremes of climatic conditions determines that the same varieties can be grown practically throughout the various cereal regions, although there are local conditions demanding special varieties.

The most recent work in wheat breeding is concerned primarily with the development of high-yielding and winter varieties for standard conditions, showing a high degree of resistance to *Puccinia glumarum*. Baking quality is not at the moment an urgent consideration, because there are already two good baking quality hybrid varieties available. The improvement of spring wheat is being attempted largely by hybridizing winter and spring types. Practically all the varieties at present in cultivation are derivatives of the old Squarehead and Squarehead's Master varieties.

The three problems exercising most attention in barley breeding are the improvement of two-row spring malting barleys, the production of two-row winter-hardy forms for malting and feeding purposes, and the improvement of the field characters of six-row forms. The improvement of two-row malting barleys involves the hybridizing of the improved types already available, the hybridization of older standard types, and, more recently, the hybridization of the two former types with the new Danish hybrids. Winter-hardiness is being introduced from continental forms, while the improvement of six-row forms has been attempted by hybridizing six-row × two-row, and six-row × six-row forms. Developmental and physiological studies in connexion with yield characters and grain quality are also being conducted. At the present moment the best two-row varieties in cultivation are derivatives of the old Archer barley.

Much of the work in oat breeding in recent years has been concerned with the production of winter-hardy forms. The work is handicapped, as is that of barley, by the scarcity of winter-hardy forms as initial breeding material. In addition to winter-hardiness, the quality (husk percentage) of the grain is also important in oat breeding. The combination of low husk percentage; large, plump grain; and strong straw, is being attempted in spring and winter types. The question of resistance to frit fly (*Oscinella frit*) is important in spring oats, and this character is being introduced from Swedish land oats. Many of the varieties at present in cultivation are derivatives of the old Probsteir oat.

21

BERGE, S. ***On the Number of Offspring Required in Genetical Experiments with Slow-breeding Animals***

In treating quantitative characters statistically, as in sire-offspring investigations, an important consideration is that of the number of individuals needed in each group, or the number of times each character has to be measured.

It is reasonable to let the number within groups have weight according to its influence on the variance between groups. We have the following formula for the variance within groups:

$$V_1 = A + \frac{V_2}{n},$$

V_1 = variance between groups; V_2 = variance within groups; n = number within groups.

If only *one* in each group be of the weight *one*, then the weight of n in each group can be found by the formula

$$p_n = \frac{A + V_2}{A + V_2/n}.$$

In this formula we can introduce the proportion between A and V_2 as T. $T = A/V_2$, and then we have the very simple formula $p_n = \frac{T+1}{T+1/n}$. T can have all values between zero and ∞. The importance of increasing the number within groups will vary proportionally. When the value of T is about zero, then the value of p_n is n. When the value of T is ∞, then the value of n is of no importance. The value of T will vary with the genetical variation in the stock examined. In a homogeneous stock the value of T will be low.

We can express the weight by the coefficient of intraclass correlation. When the number of groups and number within groups are large, then we have

$$p_n = \frac{1}{r+(1-r)/n}.$$

This last formula gives a good expression of the relationship between r and the necessary number within groups. r is affected by the genetical variation in the same degree as T. In a selected stock of high degree of homozygosis the value of r and T will be low.

Some of the external factors will decrease the value but most of them will tend to increase it. A difference in feeding and management between farms will especially tend to increase the values both of r and T, when we are examining groups of farms, because it will be increasing the value of A. On the other side good care and management will tend to decrease the value of V_2 and thereby increase r and T. We have the following formula:

$$r = \frac{A}{A+V_2}.$$

We cannot expect to find a uniform r when we are investigating groups of animals. The value will vary with the affecting factors. Usually we cannot get much further information by increasing the number within groups. We should rather try to increase the number of groups. When the number in each group is not the same in all groups, it is important to know how to calculate the average that gives us the most reliable average of the sire in question, and we can do this by using the formula for p_n.

22

BERGER, C.A. *On the Origin and Fate of Different Types of Polyploid Nuclei*

A type of polyploid nucleus, novel in behaviour and structure, has been described (Berger, 1936–9) in the larval epithelial cells of the ileum of mosquitoes. These cells and their nuclei increase in size and become highly polyploid (48-, 96- and 192-ploid). No mitotic activity accompanies this increase in size and in chromosome number. The nuclei remain in the typical resting-stage condition throughout larval life. During metamorphosis these cells undergo several successive divisions and give rise to adult tissue. At prophase multiple sister strands synapse and homologous groups of synapsed sister strands are closely paired. In late prophase these groups fall apart into their constituents with no evidence of chiasmata.

Apparently chromosomes reproduce themselves in the thin thread stage within the resting nucleus. If, after reproduction, they separate but remain extended the resting nucleus appearance is retained, as in the above case; if they separate but do not remain extended, the type described by Geitler in the salivary glands of *Gerris* may result; if, after reproduction, neither separation nor contraction occurs the increased genic material remains massed together and nuclei of the Balbiani type or of an intermediate type (terminology of Trager, 1937) result, depending on the kind of tissue and the physiological condition of the cells. This last point is evidenced by the larval mid-gut cells of mosquitoes. All the nuclei are of the intermediate type except the largest which take on the banded Balbiani-type condition just prior to their disintegration. Polyploid cells having typical resting nuclei are the only type capable of further cell division.

The structural difference between Balbiani-type nuclei in the Diptera and Geitler-type nuclei in the Heteroptera is at least not completely explained, as Geitler suggests, by the somatic pairing characteristic of the Diptera, since the polyploid nuclei of the mosquito ileum do not show somatic pairing in the resting nucleus.

The fact that multiple sisters and homologues do pair in prophase disproves the general principle of Darlington that chromosomes are attracted only in pairs and that two or more pairs repel one another.

23

BERGNER, A. DOROTHY. *Chromosome Association in* Datura

Of the ten herbaceous species included in the genus *Datura*, all have 24 as the diploid chromosome number, forming twelve bivalents at first metaphase in pollen mother cells. Tetraploid races of these species, occurring naturally or as the result of colchicine treatment, form mainly quadrivalents at M I. Sometimes twelve quadrivalents are formed but more frequently there are a varying number of bivalents, usually from two to eight. Trivalents occur when there are three chromosomes of a kind, as in triploids and primary trisomic diploids. Secondary trisomics are distinguishable because the secondary chromo-

some, having identical ends, bends back on itself to form a loop chromosome. Chains of five or more chromosomes are found in tertiary trisomics and compensating types.

In diploids, associations of four or more chromosomes in hybrids between wild races and standard testers are explained by assuming that in these races chromosome rearrangements originated through segmental interchange between non-homologous chromosomes. Such associations have been found in races belonging to seven species. A survey of over 650 geographical races of *D. stramonium* has shown that five types of interchange are widespread. Four sporadic types have also been found in the Americas. Interspecific crosses involving nine species have shown varying numbers of chromosomes in configurations, indicating that different interchanges have occurred in different species. However, in a species cross the chromosomes of the two species involved do associate somehow, either as bivalents or in larger groups. All nine species seem to have the same 24 ends of chromosomes.

The "necktie" type of association of four chromosomes, that is, two attached bivalents connected by the "hump" on each of the bivalents, may be thought of as a limiting case of segmental interchange in that the interchange is limited to satellites or the terminal portions of a chromosome. These four chromosomes may also occur as two separate closed bivalents, each with a hump, the hump indicating chiasmata that cannot be terminalized because the ends of the chromosomes are non-homologous.

Since humps are found regularly at particular ends of certain chromosomes in the standard line 1, as well as in other races where terminal portions are homologous, they must occur under additional circumstances. In cells of somatic tissue of *D. stramonium*, seven of the twelve kinds of chromosomes show secondary constrictions. Correlation between these satellited ends of somatic chromosomes with humps on meiotic chromosomes has progressed far enough to support the belief that these secondary constrictions may block the terminalization of chiasmata, with the result that these ends show humps at M I.

Another type of chromosomal rearrangement not yet found in nature but sometimes induced by X-ray and radium is the simple translocation. The new chromosome which consists of host plus fragment shows three attachment points, namely, at each end of the host chromosome and at that end of the fragment which was formerly a chromosome end. Observations at meiosis have shown that either the fragment is joined slightly subterminally to the host chromosome so that the extreme tip is free or else it is joined to the satellite. It seems that the locus of a subterminal union blocks terminalization of chiasmata formed in the host chromosome so that the latter occurs as a closed bivalent with the fragment extending outward from it like an arm.

The non-satellited end of two satellited chromosomes usually terminalizes so early that at M I there is no attachment at these ends. One end of each of two other chromosomes behaves similarly, but to a lesser extent, in intraspecific crosses of *D. stramonium*, though markedly so in interspecific crosses between *D. stramonium* and other species.

24

BERRY, R.J.A. ***An Investigation into the Mental States of the Parents and Sibs of* 1050 *Mentally Defective Persons***

Based on information from secondary sources, the parents are divided into five groups, according to their mental states. In 163 families the parents are of known normal mentality. In 202 families they were either mentally defective, insane, or of very low mentality. The latter group has produced twice as many mentally defective children as the former—54·4 % as against 26·6 %. Between these two genetically opposed groups come three others where the mental states of the parents are unknown, partially known, or very dubious. The paper concludes by pointing out the enormous financial cost to the nation of its neglect of human genetics, and concludes by suggesting that the problem is not the inheritance of mental states but of factors of growth, for mental deficiency is really a departure from the normal standards of normal growth.

25

BHADURI, P.N. ***A Study of the Relation of Chromosomes to Nucleoli in Species of* Scilla, Vicia *and* Oenothera**

A comparative study of the relation of chromosomes to nucleoli, in the light of Heitz's theory, has been made in the following plants: *Scilla nutans*, *S. sibirica*, *S. hispanica* var. Patula Excelsior, *Vicia faba*, *Oenothera Hazelae*, *O. St Jerome*, *O. angustissima*, *O. ammophiloides*, *O. Lamarckiana*, *O. blandina*, *O. Hookeri*, *O. biformiflora*, *O. biformiflora cruciata* × *O. Lamarckiana*, *O. missouriensis*, and another undescribed species of *Oenothera* collected near Moose Jaw from the Canadian Prairies. Observations were chiefly made from preparations stained with Feulgen and light green used as a differential stain for the nucleolus. A close correspondence between the number of satellites and secondary constrictions of chromosomes on the one hand and the number of

nucleoli in the somatic tissue has been established in each case. This observation has been corroborated wherever possible from nuclei undergoing meiotic divisions. The significance of such correspondence in the different species examined has been discussed in view of current hypotheses. In *Oenothera* the distinction between satellites and secondary constrictions breaks down. The number of nucleolar constrictions of chromosomes and the corresponding number of nucleoli in *Oenothera* species examined seems to be generally four. This is true, for instance, in *O. blandina*, which shows no ring formation. Four are also present in *O. Lamarckiana*, which has a catenation of $(12)+(1)_{II}$. The former species was derived from the latter by mutation. This number of constrictions and nucleoli in *Oenothera* seems to be a much older character than ring formation. The behaviour of constrictions towards Feulgen reaction has been studied in different species. The probable mechanisms underlying the organization of the nucleolus are discussed. An experimental verification as to the correspondence of the nucleolar number to nucleolar constrictions of chromosomes, as well as the fixity of the locus of organization of the nucleolus, have been shown from colchicine-treated roots of *Vicia faba*.

26

BISSCHOP, J.H.R. ***Bionomic Studies on Indigenous and Exogenous Cattle in the Semi-arid Regions of the Union of South Africa***

Since 1925, investigations have been in progress at the Veterinary Research Station "Armoedsvlakte", concerning the relation between environment and animal function. These researches have as their primary object the measuring of the effects of the collective environmental forces upon the growth, development, production and reproduction of successive grades of indigenous and exogenous breeds of cattle. At the same time the environment is being analysed so far as suitable methods are available.

The results up to date show that the Afrikaner (indigenous) grades have maintained themselves phenotypically for three generations. The higher grades of the exogenous breeds (Fries, Red Polls and Sussex) have failed to do so and are exhibiting conformational deterioration.

If animal breeding is to derive the benefit it should from bionomic researches such as described above, it is essential that:

(*a*) Workers in this field of research throughout the world should supply each other with full information concerning the methods employed by them to collect reliable experimental data, and

(*b*) If at all possible, such workers should adopt sufficiently similar experimental methods to make their work comparable.

This paper therefore supplies information about, and discusses the methods employed at Armoedsvlakte, to collect

(1) *Macro-morphological data*, such as body weights, body measurements, milk and beef production data, fertility records, etc.

(2) *Micro-morphological data*, such as chemical and biological analyses of blood, histological studies of skin, hair and bone, etc.

(3) *Data concerning the environment*, such as geology, soil chemistry, soil physics, meteorological conditions of rainfall, temperature, light, etc., analyses of natural pastures, prevalent animal diseases, systems of animal and veld management, etc.

27

BLAKESLEE, A.F. ***The Induction of Polyploids and their Genetic Significance***

INTRODUCTION

In opening our round-table discussion on the use of colchicine in inducing polyploidy, it should not be forgotten that many have made contributions in this field. It will not be possible, however, in the short time at our disposal to mention more than a few of these individual investigators. The effects of colchicine as well as other chemicals upon chromosomes in division had been studied by Dustin and associates. Lits introduced its use to the Yale laboratories where Edgar Allen applied it to the arrest of mitoses as a test of hormone activity. The speaker first heard of it in a review at a Journal Club Meeting. In the discussion which followed, he remarked that anything which made chromosomes behave differently ought to be experimented with by botanists. A little later a former assistant, Dr Eigsti, who at that time was assistant to Dr Demerec, on leaving the Department of Genetics told us he had found colchicine would double chromosome numbers in roots of several plants with which he had experimented. He suggested we try it with Daturas. We told him we had been planning to do so, but in view of our earlier experiments with chloral hydrate and with other agents in efforts to induce tetraploidy we could not be very hopeful. Nemec, it will be remembered, induced doubling of chromosome numbers in roots with chloral hydrate as early as 1904. Chromosome numbers appear capable of doubling up rather readily in roots. We have frequently found, for example, that the roots of our haploid plants have been partially or wholly diploid. It appears a much more difficult task,

however, to induce doubling of chromosomes in the shoots which alone are capable of producing flowers and seeds and thus giving rise to tetraploid races.

The seed had proven to be a convenient part of the plant to treat in the induction of gene and chromosome mutations. Seeds of *Datura* were accordingly used in tests with colchicine along with a number of other chemicals. As soon as the seeds which had been treated with colchicine had germinated, the swollen stems of the seedlings made us believe we had at last found a method of inducing tetraploids. This belief became a certainty in our minds when the seedlings produced leaves roughened in a way characteristic of spontaneous tetraploids. The larger pollen grains produced by such rough-leaved sectors and the actual demonstration that their buds contained 4*n* chromosomes were final proofs of tetraploidy which were hardly necessary to those familiar with the appearance of tetraploids. At about the same time, in fact they had begun their experiments somewhat earlier, the Nebels had independently been investigating the effects of colchicine on the behaviour of plant chromosomes with the intention of utilizing colchicine in the induction of polyploidy. Perhaps there were others. At any rate it was an obvious next step to test on plant cells a chemical substance which the zoologists had shown to have such peculiar effects upon animal chromosomes. Who happened to induce the first tetraploid with colchicine is of indifference to genetics. In any case, its use in plant breeding could not have been long delayed.

Methods

In using colchicine a variety of methods have been employed. Some of these have been reported on by Avery and the speaker. The essential thing is to affect the meristematic regions which are to give rise to shoots and ultimately to flowers. In our experience it is easier to get 4*n* sectors by soaking seeds in appropriate concentrations of colchicine before planting than by treating other parts of the plant. However, seeds cannot be used, for example, with forms which reproduce only vegetatively, such as sterile hybrids. Seed-treated seedlings show swollen hypocotyls and inhibited root formation. Preliminary tests with growth-promoting substances such as indol-butyric acid have not in our experience proven of value in overcoming the check to root development. There appears a wide range of susceptibility to colchicine treatment. For seeds of *Datura stramonium* a 0·4 % solution of colchicine for 4 days is a moderate dose, whereas a 0·0004 % solution with seeds of *Portulaca* will give a distinct reaction. Seedlings are best treated in the cotyledon stage by applying drops of the solution on the young plumule. With *Datura* this method leads to distinctly roughened leaves, but the shoots soon recover and revert to the diploid condition. When buds are treated, the effect seldom travels far beyond the portion actually touched by the solutions. The first effect is generally to inhibit the growth of the parts affected and to cause the outgrowth of untreated dormant buds. If the growth from these latter is kept removed, the affected buds may be forced to develop. In spraying buds of certain species we found apparent difficulty in getting the buds properly wetted. In consequence we tried using the colchicine in solution with "Vatsol", an effective substance for lowering surface tension, but with little if any improvement. Lanolin as a carrier of the colchicine was early discarded, since it is inconvenient in use and makes a quantitative determination of the dose difficult.

An emulsion with lanolin which can be used as a paste or more conveniently applied as a spray when diluted to the consistency of thin cream has been found to be much more effective than water solutions. For example, a test showed that spraying a series of plants with an emulsion containing 0·4 % colchicine two times with an interval of 3 days between applications was more effective than spraying with a 0·8 % aqueous solution of colchicine twice a day for 2 weeks. The emulsion we have used keeps unaltered under laboratory conditions, at least for several months. Although some species are relatively resistant to the spray method, the chromosomes of others are readily doubled. Thus of six plants of the shepherd's purse (*Capsella bursa-pastoris*), which in the rosette stage had received only a single application of an emulsion spray containing 0·4 % colchicine, five produced shoots with 4*n* flowers and capsules. Peto has found it convenient to cover the bud to be treated with a gelatine capsule containing a solution of colchicine in agar. The monocotyledons as a class seem difficult to treat successfully, in part perhaps because their growing points are often protected by sheathing leaves which prevent the solutions reaching the cells which give rise to the shoots where the 4*n* cells are of value to the plant breeder. Sears has told us he has doubled the chromosomes in suckers of wheat hybrids by laying pledgets of cotton soaked with colchicine solutions around the base of the seedlings where suckers were expected to develop. By this method he avoided the checking of root growth which results from treating seeds at or before germination. Myers has succeeded in getting tetraploids of several species of *Lolium*. A method which he suggests is the injection of colchicine solution inside the leaf sheaths which surround the growing points. Cullen has succeeded in inducing tetraploids of barley by treating their flower heads about 24 hr. after pollination. The seeds which developed from such treated heads had 4*n* sectors from which tetraploid

races were developed. It is evident that different kinds of plants differ both in respect to the concentration of colchicine and in respect to the particular method which is most effective. The individual investigator is in best position to choose a method adapted to the form with which he is working.

So far we have doubled the chromosome numbers in seventy different kinds of flowering plants included in forty-eight different species, twenty-nine genera and sixteen families. If the work of other investigators were included these numbers would probably be more than doubled. The only form among flowering plants in which the chromosomes appear entirely immune to colchicine treatment is the plant *Colchicum*, from which the alkaloid is secured. Among the lower forms Miss Satina has doubled the chromosomes of the liverwort *Marchantia* and has thus secured both male and female $2n$ thalli. The fungi and bacteria, however, appear immune. In some cases Dr Conklin has shown that they utilize colchicine as a source of nitrogen.

Colchicine is not the only chemical which is capable of inducing tetraploidy but it appears to be by far the best yet discovered. In our experience, acenaphthene used by Kostoff is relatively ineffective. We have induced tetraploids in *Portulaca* by treatment with sodium cacodylate, but this substance did not work with *Datura*. Randolph has been successful in inducing tetraploidy in maize by means of heat treatments shortly after fertilization. Heat may still be a useful method in special cases. With certain Solanaceae regeneration from the callus after decapitation has yielded some tetraploids. Lindstrom and Greenleaf are the most recent users of this technique to induce doubling of chromosome numbers.

Characteristics of tetraploids

In discussing tetraploids, a distinction should be made between the first generation in which they appear and later generations. In our experience tetraploids of *Datura*, whether induced or spontaneous, always appear as somatic mutations and not as tetraploid plants derived from a $4n$ egg. In this generation the tetraploid tissue generally shows as sectors in which $4n$ and $2n$ cells are intermingled to form a mixochimera distinguished by characteristically roughened leaves. Later these rough-leaved sectors may grow out into smooth-leaved $2n$ or $4n$ branches. In the next generation the plants have smooth leaves since their cells should all have the same chromosome number as the zygote. The characteristic of tetraploids of most interest to many is the increased size of their flowers. The series of flowers of $1n$, $2n$, $3n$ and $4n$ *Datura stramonium* shows clearly that there is an orderly increase in floral size with increase in chromosome number. This summer we had growing in the garden a series of $2n$ and $4n$ plants of *Petunia* derived respectively from an untreated $2n$ and an induced $4n$ branch of a single parent. In order to show the difference between a $4n$ and a $2n$ flower we photographed the first $4n$ flower that showed in our cultures in contrast with a normal $2n$ control. These are shown in Fig. 1. The relative size of the $4n$ flower on the right

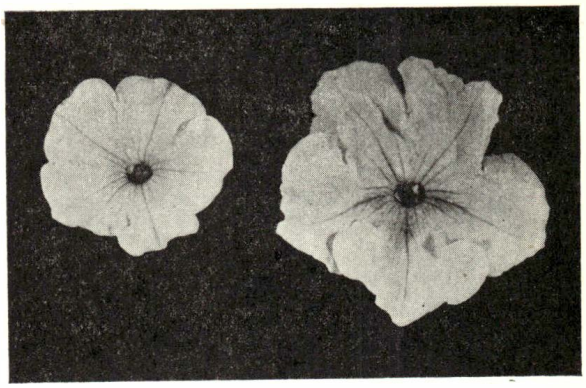

Fig. 1. Flowers of garden *Petunia*; on the left a normal $2n$ control, on the right the first flower from our $4n$ cultures.

suggested the enthusiastic representation of a new variety in a flower-seed catalogue, and we became suspicious that a single flower, even though chosen at random, might not be typical. We therefore took photographs of what appeared to be typical flowers of twelve tetraploid plants together with flowers from twelve diploid controls as well as twelve flowers from a single typical $4n$ plant alongside twelve flowers from a single $2n$ control. This latter photograph is reproduced as Fig. 2. It will be seen that on the average the $4n$ flowers on the right are larger than the $2n$ controls, although there is considerable difference in size of flowers from the same plant due to environmental factors. This is the usual condition. In some forms, however, the environmental factors appear more important than the number of chromosomes. Tetraploid and diploid flowers of *Portulaca*, for example, cannot be distinguished by size of flowers alone. Other exceptions may be expected to the rule that doubling chromosome numbers brings about a distinct increase in size of flowers.

In *Portulaca* we have an example of new floral types brought about by tetraploidy. In this species double flowers (D) is dominant to singles (d). Full doubles (D_2) do not set seed; semi-doubles (Dd), however, are fully fertile. In diploids there are two types of doubles (D_2 and Dd); in tetraploids there may be four. These are shown in Fig. 3. The two new double types are D_3d and Dd_3. The homozygous tetraploid (D_4) does not set seed but the triplex type (D_3d) is fertile. If segregation in this case is in accord with random assortment of four chromosomes, the plant

breeder could guarantee that all the seeds from selfing triplex plants would produce high-grade doubles. If segregation followed random assortment of eight chromatids there should be not over 0·13 % singles.

Among characteristics of value as short-cut methods of identifying members of the polyploid series the best are the peculiarities of their pollen. Illustrations may be taken from *Datura*. The pollen grains of a haploid (1*n*) are nearly 90 % aborted, and the good grains are all of the same size. Pollen of a diploid (2*n*) is relatively good with usually less than 1 % aborted. The pollen grains of a tetraploid (4*n*)

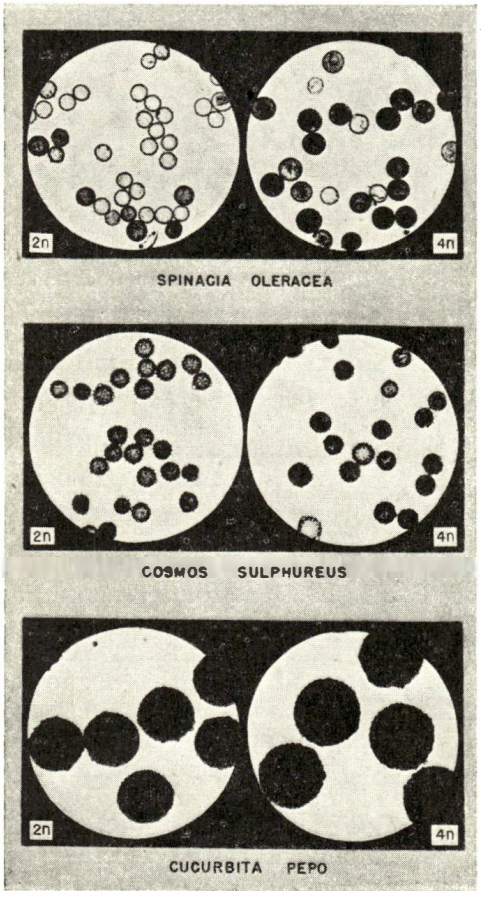

Fig. 4. Pollen of three species, in each case the pollen on the right is from a tetraploid, that on the left from a 2*n* control.

have approximately twice the volume of those of a diploid and upwards of 4 % are aborted. About half of the pollen grains of a triploid (3*n*) are aborted and the good grains range in size from the 2*n* grains of a tetraploid to the 1*n* grains of a diploid. In Fig. 4 are shown photographs of pollen from 2*n* and 4*n* flowers of a number of species. We have found as yet no exception to the rule that grains of a tetraploid are distinctly larger than those of a diploid. In *D. stramonium* we have two 4*n* lines which have been inbred through selfing for thirteen and fourteen generations respectively. Measurements made this summer show that their pollen grains are the same size as those of 4*n* plants which were the immediate offspring of induced tetraploids.

Under certain conditions the pollen test cannot be applied. This is true of female plants of dioecious species. In hemp we were able to distinguish diploid and tetraploid branches on treated female individuals by the relative size of the stomata on floral bracts. The size of guard cells as a criterion of tetraploidy must be used with caution to ensure that the tissues from which the stomata are taken are comparable. Peto has plotted the size of stomata on each leaf from the lowest to the highest for 2*n* and 4*n* individuals of one of the grasses. On comparable leaves the 4*n* stomata were always larger, but leaves could be chosen for comparison in such a way that the 2*n* stomata were larger. Differences in stomatal size from comparable leaves of *D. stramonium* are shown in Fig. 13.

The seeds of tetraploids are regularly larger than those of diploids as shown in Fig. 5. The number of

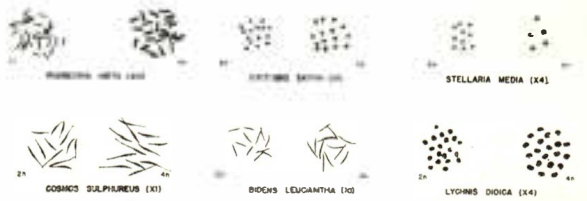

Fig. 5. Seeds of six species. In each case tetraploid seeds on the right and diploid controls on the left. Figure was rephotographed from an exhibition chart and magnifications should be disregarded.

seeds in a tetraploid capsule is generally reduced. Fig. 6 shows photographs of a series of capsules of *D. stramonium* together with their contents. There appears to be a progressive shortening and thickening of the capsule with increase in chromosome number. The seeds of haploid capsules are none or very few, those of diploids abundant, those of triploids scanty with considerable size variation, those of tetraploids larger than those of diploids and limited in number. The hexaploid capsule which had been induced by spraying a 3*n* plant shows only a single large seed which failed to germinate. Octoploid capsules, of which we have secured several both by treating 2*n* and 4*n* material, have never produced more than abortive ovules. How many times the chromosomes may be doubled to give viable races must be determined for each species. The only ± 8*n* plants which we have secured in the second generation are in *Portulaca parana*. An especially interesting series of

differences in fruit shape is found in the cucurbits which Sinnott has been studying in co-operation with us. In one case tetraploidy changes a pear-shaped fruit to a disk, a difference which in diploids is brought about by a single gene. In another case (the bottle gourd) tetraploidy has eliminated the neck entirely.

Polyploidy and sex

The finding by Hagerup of a $4n$ hermaphroditic species, *Empetrum hermaphroditum*, which was believed to have originated from the related dioecious species *E. nigrum*, gave presumption to the belief that doubling the chromosome number of a dioecious species would result in an hermaphroditic form. Furthermore, it has been stated by a number of *Drosophila* investigators that tetraploidy could have played no role in the evolution of dioecious species on account of difficulties that would arise in the chromosome mechanism of sex determination. It was for these reasons that we started in co-operation with Warmke tests of the effects of induced tetraploidy in a series of dioecious species of plants. In *Melandrium* we were able to show that doubling chromosome numbers ultimately leads to a balanced tetraploid population with approximately equal numbers of male (*XXXY*) and female (*XXXX*) individuals. It would appear therefore that doubling chromosome number does not necessarily lead to hermaphroditism, and that in the species most carefully studied there is nothing in the chromosome mechanism that would prevent tetraploidy from playing a role in evolution of a dioecious species in nature as it has played a role in the evolution of a constant dioecious race in our laboratory cultures. As a matter of fact there are species of *Salix* which have twice as many chromosomes as other species in the genus, and the same is true of the genus *Valisneria*.

Multiple diploids

Of most interest from the evolutionary standpoint as well as from their potential economic value, are the multiple diploids which may be formed from sterile species hybrids by doubling their chromosome numbers. The species hybrid *Nicotiana sylvestris* × *N. glutinosa* is sterile with nearly 100 % aborted pollen because the chromosomes of the first parent are unable to mate up and form pairs with those of the second parent. Since it has only one of each kind of chromosome, the sterile hybrid is in fact a haploid ($1n$), and being a hybrid between two different species it may be regarded as double haploid $2(1n)$. When the chromosomes are induced to double in number, each chromosome will have a mate from its own parent with which to pair and the plant will become fertile. Since it has two of each kind of chromosomes it is a diploid, and since it is a hybrid between two species it may be called a double diploid $2(2n)$. By hybridizing *N. tabacum* which is already a double diploid with *N. glutinosa* and doubling the chromosomes of the resulting sterile hybrid we have secured a fertile triple diploid $3(2n)$. By doubling the chromosomes of a double diploid, one should obtain a double tetraploid $2(4n)$ with four chromosomes of each kind. The terminology we have been using has been discussed with illustrations elsewhere. It seems preferable to base our terms upon the numbers of homologous chromosomes rather than upon the total number as has often been done. It must be admitted, however, that no logical and convenient system seems possible that will take account of all the types of chromosome duplication which are already known to have occurred. A simple test for the production of fertile double diploid flowers from a sterile hybrid is the presence of good grains in place of aborted pollen. The difference in the pollen may be seen even without the aid of a microscope. A still simpler indication that the chromosome number has been doubled is the setting of capsules and production of seed which is not possible in the sterile hybrid.

The fact that our most valuable wheats, oats, tobacco and cotton are multiple diploids leads to the belief that the induction of multiple diploidy is likely to be of increasing significance in the production of new varieties and species of economic importance.

We have been discussing the transformation of a sterile into a fertile form through doubling chromosome numbers when the sterility is due to complete incompatibility between the chromosomes of the parents of the sterile hybrid. Since sterility may be brought about by a number of different causes, we should not expect to be always able to relieve it by doubling the chromosome number. We have in *Datura* an example of a considerable reduction in the amount of pollen sterility through doubling the number of chromosomes. In Fig. 7 is shown on the left a $2n$ flower of the species hybrid *D. metel* × *D. meteloides*. The cross between these two species is very difficult to make, and up to the present summer only a single hybrid plant had been secured from several hundred pollinations. At metaphase the hybrid shows two circles of 8, one circle of 4 and two pairs of chromosomes. The circles tend to break prematurely, as is often the case in species hybrids, and the chromosomes to align themselves on the spindles as unequal pairs and singles. In consequence chromosome deficiencies are brought into the developing pollen mother cells with a resulting high percentage ($\pm$ 85 %) of pollen abortion. On the right in Fig. 7 is shown a $4n$ flower from a branch of the hybrid in which the chromosomes had been doubled by spraying the plant with colchicine emulsion. The plant had

proven rather resistant to treatment, and it was only after about a year's intermittent attempts that we succeeded in getting a branch all the flowers of which

Fig. 12. A hapoid (1*n*) branch of *Datura starmonium* with 2*n* capsules which had been induced by colchicine treatment.

were tetraploid. The tetraploid flower shown in the photograph is only slightly larger than the 2*n* control on the left. The corolla, however, was of considerably thicker texture. It will be noticed that the filaments of the stamens are thicker and the style much shorter than in the 2*n* flower. The chromosomes of the 4*n* hybrid have not yet been studied. It is probable that parental chromosomes in the tetraploid tend to assort together with reduction of deficient combinations. At any rate, the pollen abortion has been reduced to only about 25 %. Fig. 8 shows pollen of the 4*n* hybrid on the right in comparison with that of the highly sterile 2*n* hybrid on the left.

An example may be given of rendering a sterile hybrid fertile when the cause of the sterility is unknown. Marsden-Jones and Weiss reported sterile hybrids between the closely related subspecies *Anagallis arvensis phoenicia* × *A. arvensis foemina*, except when the former was the salmon-flowered variety, in which case the hybrids were fertile. We suggested to Prof. Weiss that he test the effects upon the sterility of doubling the chromosome number. He sent us seeds to produce the hybrids and asked us to make the tests. The species proved to be very susceptible to treatment. Fig. 9 shows an untreated seedling of the sterile hybrid on the left, and on the right a seedling the terminal shoot of which had been sprayed a single time with an emulsion containing 0·4 % colchicine. The leaves of the treated branch were characteristically thickened and the growth in this region checked. By cutting off the vigorous shoots which grew from the untreated buds below, growth was induced from the treated region. The chromosomes have not yet been counted, but judging from the appearance of the leaves on some of these branches their chromosomes had been doubled. Good pollen from flowers on such branches are shown on the right in Fig. 10 in comparison with aborted pollen of the untreated sterile hybrid. Flowers with good pollen produced capsules with good seeds (Fig. 11, right), while the flowers of the controls (Fig. 11, left) fell off without setting fruit. It will be seen that even the pollen test is not necessary to determine that the sterile hybrid has been rendered fertile by colchicine treatment.

Method of securing pure lines

To the plant breeder who wishes to combine desirable characters from two distantly related forms, the most expensive and time-consuming part of the process is likely to be the isolation of homozygous races in F_2 and later generations. Through the use of colchicine it may ultimately become possible to simplify considerably the process. The occurrence of

haploids is not infrequent in *Datura*. Since 1922 we have recorded 220 in our cultures. It is not known what the stimulus may be which causes them to develop from reduced eggs without fertilization, although in some but not all cases the haploid has been derived from one of two twin embryos. Without treatment, haploids can be made to produce $2n$ seed with relative difficulty. In certain lines attempts have been complete failures. By spraying a haploid with colchicine emulsions, however, an abundant production of $2n$ capsules results, as may be seen in Fig. 12. The selfed offspring of a haploid of course must be homozygous, barring new mutations, since each single chromosome will be duplicated. We have solved only half the problem, however. We are attempting to find a method of inducing the production of haploids through parthenogenesis of reduced ovules. If that could be done we should be able in two jumps to secure pure lines from highly heterozygous material.

Chromosome deficiencies from colchicine treatment

In the previous part of this talk we have spoken as if the only result of colchicine treatment was a doubling of the full complement of chromosomes within the cells affected. That this was not the case was early suspected by the appearance of some of the abnormal sectors in our cultures. Dr Bergner has found that colchicine may cause elimination of individual chromosomes either before doubling to form $2n$-1 sectors or after doubling to form $4n$-1 sectors. She has found as many as six chromosomes missing from the forty-eight of a normal $4n$ condition. Frequently the doubling occurs after elimination to form $4n$-2 types in which two chromosomes are missing from the same set. In forms in which vegetative reproduction is possible those chromosomal deficiencies which may be obtained by colchicine treatment offer an increased range of chromosomal types some of which may prove of economic importance.

Induced periclinal chimeras

It has been our practice to help in the identification of induced tetraploids by an inspection of the pollen. In many cases the size of the pollen grains did not agree with what would be expected from the appearance of the leaves and capsules. The pollen might be that of a diploid, and microscopic examination shows $2n$ chromosomes in pollen mother cells and yet the sector looks like a tetraploid. The generative tissue was thus clearly $2n$. That the epidermis was $4n$ was evident from the size of the stomata shown in Fig. 13. Miss Satina has been making a detailed study of selected cases of such periclinal chimeras. In sections through the actively growing regions it is possible to identify $2n$ from $4n$ tissue by chromosome counts in dividing cells. When one tissue is $8n$ it may be easily distinguished from $2n$ tissue by size of cells alone. The most frequent type of periclinal chimeras has a $4n$ epidermis and a $2n$ inner tissue, but a type has been found with $2n$ epidermis and $4n$ inner tissue. A couple of cases have been found in which an $8n$ epidermis enclosed $2n$ tissue. By thus labelling the different tissue elements by differences in chromosomal constitution, it is being possible to follow the contribution made by the germinal layers to adult

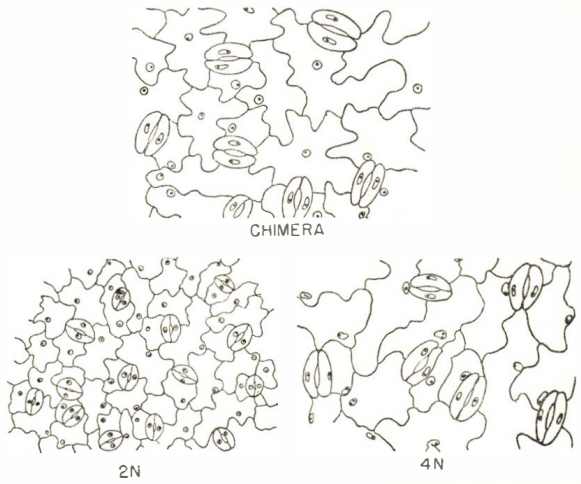

Fig. 13. Drawings of surface view of leaf epidermis with stomata; above from a periclinal chimera with $4n$ epidermis and $2n$ internal tissue; below, right from a $4n$ leaf, left from a $2n$ leaf.

structures. It appears, for example, that the dermatogen is a definite germinal layer which forms the epidermis but that it also contributes to cells inside the leaves, sepals, petals, stamens and pistil.

The discovery of periclinal chimeras justifies us in our practice of carrying an induced tetraploid to the second generation before considering it an established tetraploid.

Induction of extra-chromosomal types

The ability to induce tetraploids at will opens up the possibility of securing a considerable number of other chromosome types. The cross $4n \times 2n$ should give $3n$ offspring. A triploid is of interest as a member of the polyploid series. Seed production is scanty at best, and triploids of a given species may continue flowering throughout the season whereas the diploid individuals are soon set up with capsules and cease flowering. Triploids are also of interest as the source of extra chromosomal types. The cross $3n \times 2n$ should give the full range of primary $2n+1$ types as well as a considerable number of double trisomic $2n+1+1$ types.

CONCLUSIONS

Heretofore conclusions regarding the effects of polyploidy have had to be drawn for the most part from species in nature which differ in chromosome numbers or from occasional spontaneous occurrences of tetraploids in races which were far from homozygous. It is now possible to induce polyploidy in controlled material, and from its study to establish general laws regarding the effects, physiological as well as morphological, which are brought about by duplication of chromosomes.

28

BLARINGHEM, L. ***Hérédité et Évolution chez les Plantes***

L'ajustement des dénombrements aux règles numériques de Mendel nécessite souvent la subdivision en multiples unités des éléments essentiels d'un couple défini de caractères. Il me paraît difficile de tenir compte, au point de vue de l'Évolution, des solutions qui font intervenir plus de trois couples d'unités à moins que les preuves ne portent sur des milliers de descendants (F_2).

L'examen des faits expliqués par l'interaction de deux couples d'unités dorme en grande sécurité; le cas le plus simple, d'un seul couple, est précisément celui qui donne aux règles numériques la valeur d'une loi, forme particulière du postulat général de la probabilité à chances égales. Cette loi est strictement suivie pour les échanges de réserves amylacées des Pois de Mendel, des maïs de H. de Vries où la Xénie trahit la substitution régulière avec dominance totale en (F_1). Il ne s'agit ici que de dominance et de ségrégation diastases, ou plutôt d'états d'activité bien définis de la même diastase. Cette catégorie de preuves n'a aucun rapport avec l'Évolution.

La substitution qui fait intervenir des complexes de caractères liés entre eux fournissent par contre des indications précises sur les affinités des types, variétés ou jordanons, dans l'espèce. L'interprétation selon le schema mendelian des croisements liés aux sexes, des croisements qui entraînent la Hérédité partielle correspond presque toujours à la présence sur le même individu de mosaïques; certaines de ces mosaïques limitées à un petit nombre de cellules peuvent acquérir un équilibre durable et fournir des mutations. Il faut reconnaître que les conditions de développement, que le milieu, que l'âge jouent un rôle décisif dans la formation et la fréquence de ces mosaïques; par là s'expliquent de nombreux cas d'adaptation. Des faits précis illustreront ces trois points.

29

BOERGER, A. ***Angewandte Genetik als entscheidender Faktor für das Vordringen des Weizenbaues im subtropischen Osten Südamerikas***

Im subtropischen Osten Südamerikas sind die klimatischen Gegebenheiten als der für den Weizenbau im Minimum befindliche Vegetationsfaktor zu bezeichnen. Die Südgrenze des argentinischen Weizenbaues liegt etwa bei Bahia Blanca (40° südl. Breite). Brasilien, das jährlich rund eine Million Tonnen Weizen einführt, förderte letzthin den Weizenbau zunächst in seinen Südstaaten und macht nun auch den Versuch, ihn bis in die Höhenlagen nördlicher Staaten (Minas Geraes und Goyaz) also bis zum 10. Grad äquatorwärts vorzuschieben. Uruguay, das mit La Estanzuela den Anstoss für die Züchtung von Weizen gegeben hat, die diesen besonderen Klima-Anforderungen angepasst sind, liegt zwischen dem 30. und 35. Grad. Die mittlere Jahrestemperatur beträgt 16·1 Grad, die mittlere Niederschlagsmenge 969 mm. (Montevideo).

Diese grosse räumliche Ausdehnung erfordert selbstverständlich strichweise wechselnde Zuchtrichtung. Es hat sich aber gezeigt, dass die vordringlichste Zuchtrichtung La Estanzuelas: eine weitgespannte Saatzeit (Mai bis August) ohne grosse Ertragseinbusse, auch das beste Auslesemoment für eine grosse ökologische Streubreite war. Im Staate Rio Grande do Sul konnten sich daher die Versuchsstationen Bagé und Alfredo Chaves in ihrer Züchtungsarbeit auf die in Uruguay geschaffenen Weizen "Centenario" und "Porvenir" stützen. Der in Bagé gezüchtete Weizen "Fronteira" hinwiederum brachte auch in weiter nördlich gelegenen Staaten noch durchaus befriedigende Erträge. Besonders aussichtsreich scheinen Kreuzungen von "Fronteira" und "Centenario" zu sein.

In Bezug auf das Qualitätsproblem unterscheiden sich Uruguay und Brasilien insofern von Argentinien als sie in erster Linie Sorten benötigen, die ohne Verschnitt mit Verstärkungsweizen oder chemischen Zusatz gute Backfähigkeit besitzen.

Seit 1929 verlangt die Rostresistenz ganz besondere Beachtung. Die damals erstmalig auftretende Gelbrostepidemie vernichtete einige Typen vollkommen. Eine Rostepidemie soll vor einem Jahrhundert auch in Rio Grande do Sul die früher schon zu verhältnismässig grosser Bedeutung gelangten Weizenkulturen der kolonialportugiesischen Zeit gänzlich vernichtet haben. Die Auslese auf Ustilago-Resistenz führte in La Estanzuela zur Schaffung des praktisch immunen "Litoral". Daneben hat sich Warmwasserbehandlung als äusserst wirtschaftlich erwiesen.

Dürreresistenz ist in Uruguay weniger wichtig. Ein weiter nördlich betriebener Weizenbau muss aber

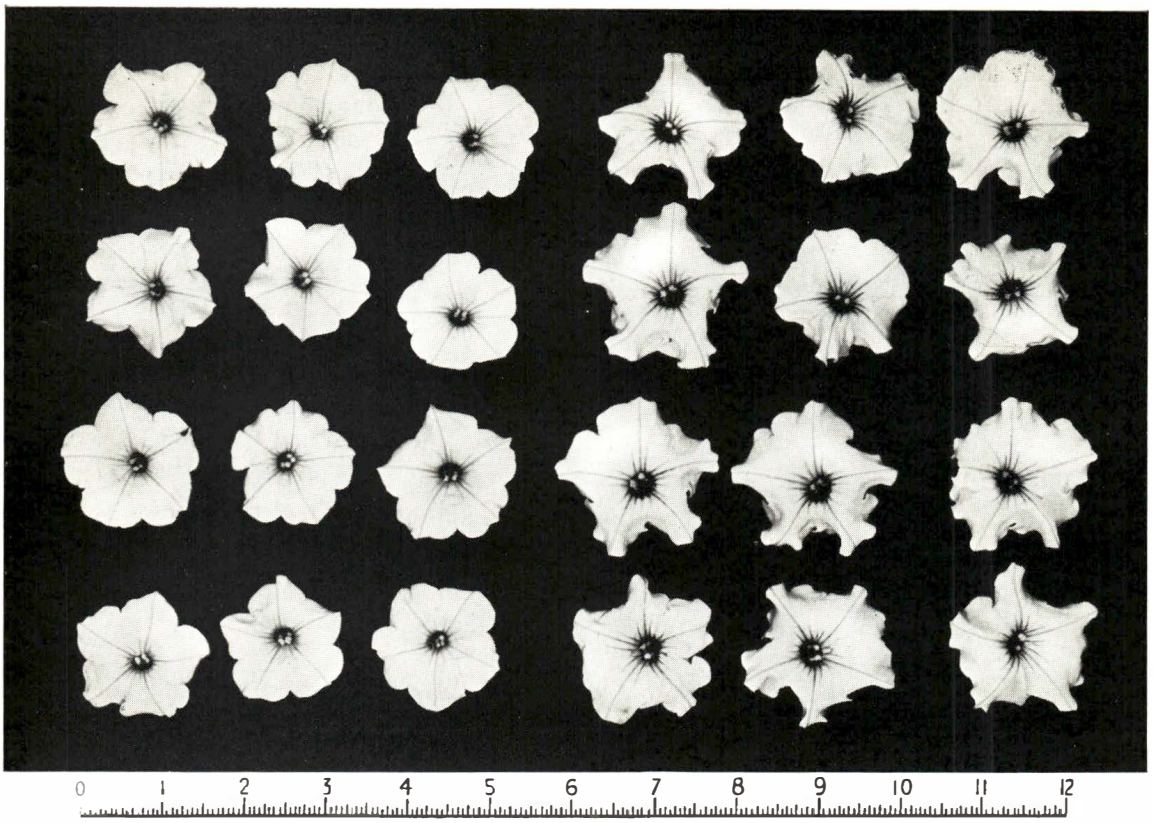

Fig. 2. Flowers of garden *Petunia*; the 12 on left from a single 2*n* plant, the 12 on the right from a single comparable 4*n* plant.

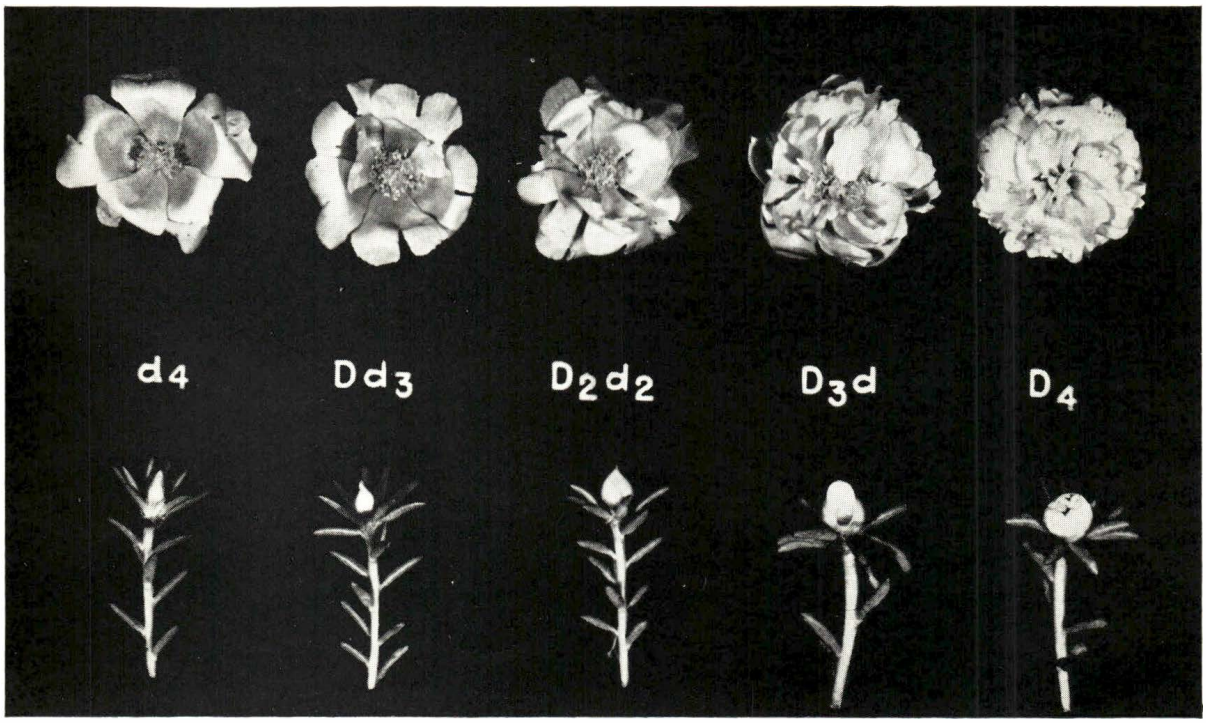

PLATE I. Fig. 3. Different types of double flowers from a segregating culture of tetraploid *Portulaca grandiflora*.

A. F. Blakeslee (Paper 27)

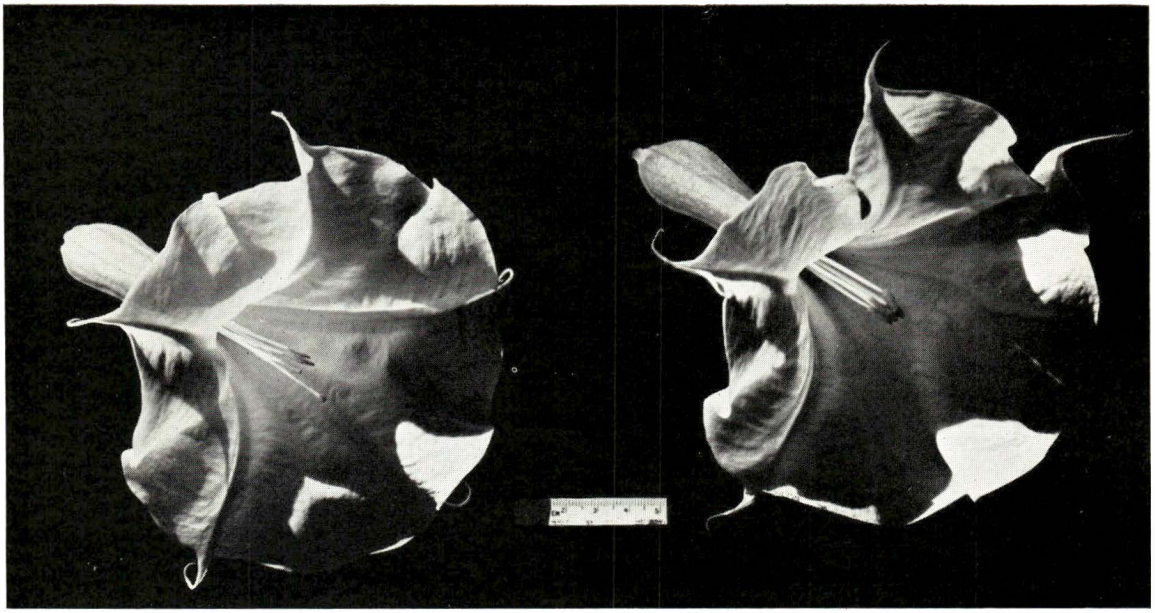

Fig. 7. Flowers of the species hybrid *D. metel* + *D. meteloides*; on left from 2*n* branch, on right from 4*n* branch.

Fig. 9. Sterile hybrid *Anagallis arvensis phoenicea* + *A. a. foemina*; on left control, on right treated seedling.

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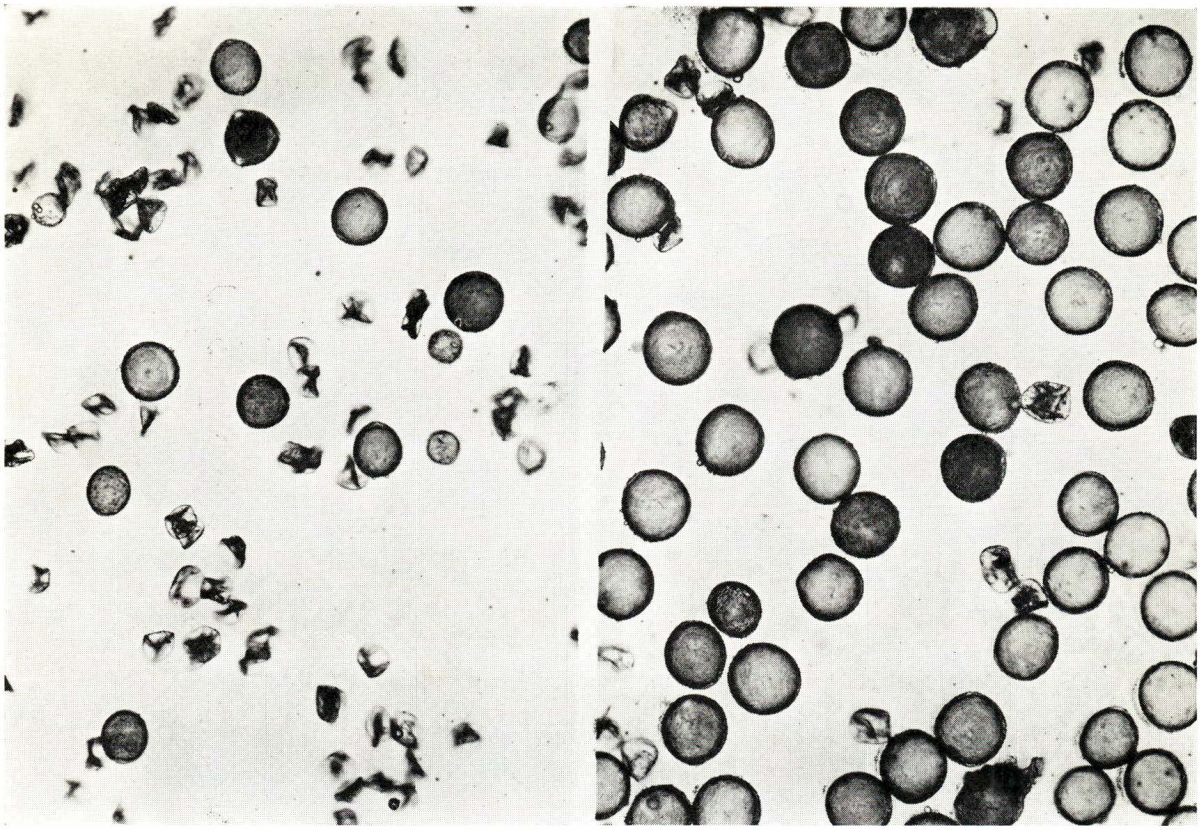

Fig. 8. Pollen of species hybrid *D. metel*+ *D. meteloides*; on left from 2*n* flower, on right from 4*n* flower.

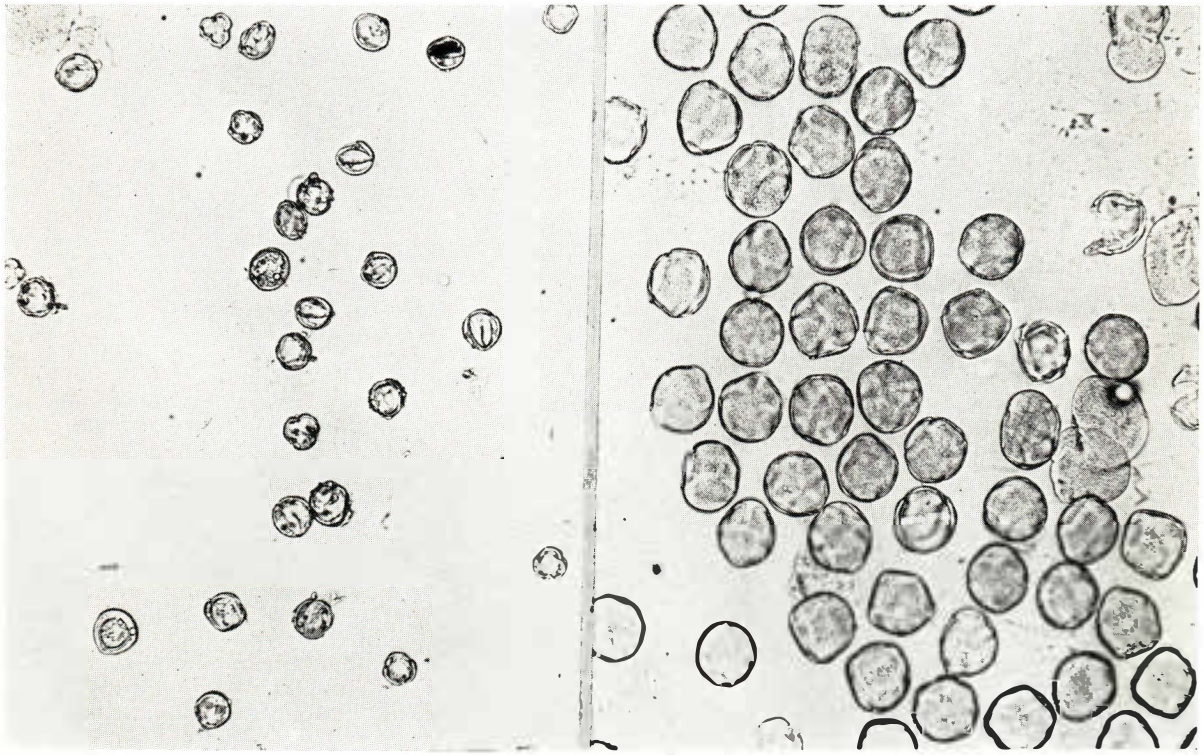

Fig. 10. Pollen of *Anagallis* hybrid; on left from sterile hybrid, on right from fertile treated branch.

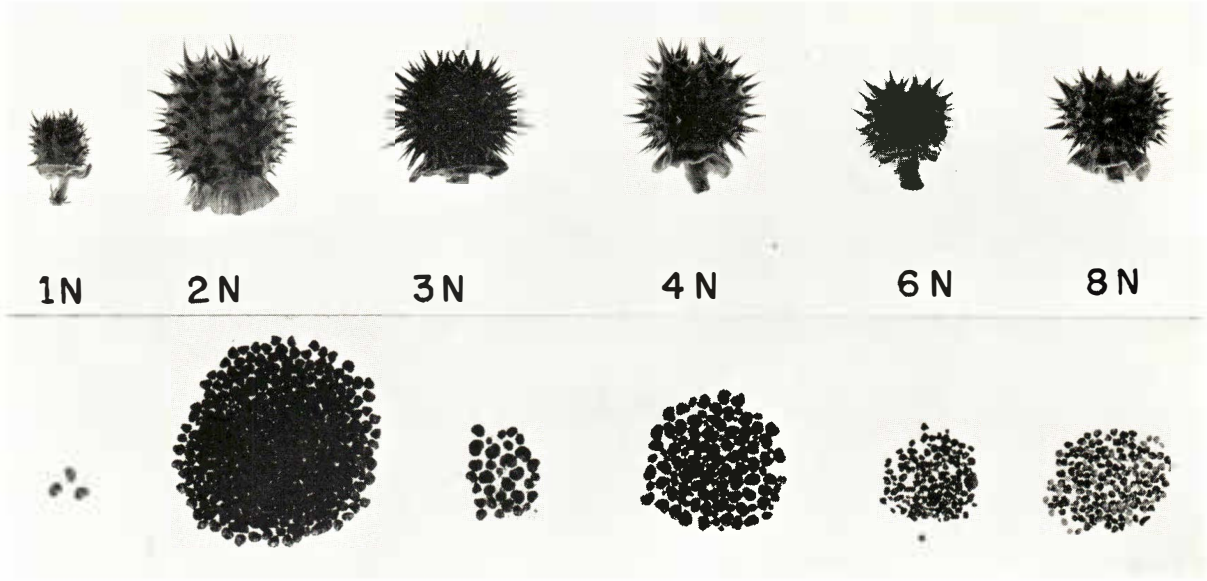

Fig. 6. Capsules from a polyploid series in *Datura stramonium*. Below each is shown the contents of the capsule.

Fig. 11. *Anagallis* hybrid; sterile hybrid on left, branch rendered fertile by colchicine on right.

A. F. Blakeslee (Paper 27)

nachdrücklich auf Frühreife züchten, um den früh einsetzenden hohen Temperaturen der heissen Jahreszeit wirksam zu begegnen.

Durch die Schaffung der für weitgespannte Saatzeit geeigneten Weizen ergab sich in Uruguay Sicherung gegen:

(1) Ernteverminderung bei Spätsaat in Regenwintern.

(2) Verheerende Schädigungen bei Auftreten des Getreideflohes (*Toxoptera graminum*).

(3) Ertragseinbusse durch Fusskrankheiten.

Die Schaffung von Weizen, die diesen vielseitigen Anforderungen weitgehend gerecht werden, wirkte sich deutlich in der Entwicklung des uruguayischen Weizenbaues aus. Die Anbaufläche dehnte sich trotz der für eine extensive Viehzucht sehr günstigen Bedingungen von etwa 275,000 ha im Jahre 1919–20 auf über 500,000 ha im Jahre 1938–9 aus. Noch deutlicher zeigt sich der Züchtungserfolg in den Landesdurchschnittserträgen. Die Jahrzehntsmittel stiegen um 33 % wie folgt:

1911–20	571 kg./ha.
1921–30	760 kg./ha.

In den auf eine längere Züchtungsarbeit zurückblickenden Gebieten Südamerikas zeigt sich somit deutlich der Einfluss der angewandten Genetik auf die Ausdehnung des Weizenbaues. Da die brasilianische Bundesregierung diese Arbeiten nunmehr auf breitester Grundlage auszubauen beabsichtigt, ist mit einem weiteren Vordringen des Weizenbaues äquatorwärts in den grundsätzlich für diese Kultur sich eignenden Höhenlagen verschiedener Staaten bis in den Tropengürtel hinein zu rechnen.

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BONADONNA, T. ***The Work done on Artificial Insemination in Italy***

A brief description is given of the work done in Italy since Spallanzani (1780) up to the establishment of the Institutes for artificial insemination at Milan and Bologna in 1937. The former, the Lazzano Spallanzani Institute, has now subsidiary institutes, and by legislation the Department of Public Health controls the organization of local centres for artificial insemination. About 100 of these centres are now working in Italy and the Colonies, about 80 % of their activities being with cattle.

Artificial insemination is used chiefly to overcome sterility and any shortage of suitable males in some areas, and also as a means of combating genital diseases transmitted in coitus. The methods of semen collection and storage are described. In 1938 and 1939 about 20,000 females have been inseminated artificially. In cattle pregnancy has been obtained in 60–80 % of cases with single inseminations and up to 90 % from one, two, or three inseminations; in sheep 80–90 % even with diluted semen; in mares 70–80 % when more than one insemination has been possible in one heat period; in sows about 90 % with whole or diluted semen; and in hens it is possible to get 90–100 % fertile eggs when the semen is injected into the oviduct. The present techniques of sperm storage and control could be improved, but the method of Walton and Edwards has been found rational.

The advantages of artificial insemination under various conditions are discussed, including, for example, for mule breeding and for the production of Karakul pelts.

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BONNEVIE, K. ***The Manifestation of Hydrocephalus in Mice***

An investigation of the hydrocephalous mutation (appeared 1932) in Clark's mice stock has been made. The *genetical analysis* of this recessive mutation proves to be complicated not only by the varying manifestation of the anomaly but also by the occurrence of heterozygotes behaving as if more than one gene-pair were involved. A genetical analysis will be given in the paper.

An *embryological analysis* of the hydrocephaly—enlargement of the head due to an excess of cerebrospinal fluid, both inside the brain ventricles and in the subarachnoid space—shows that its *typical manifestation*, beginning in embryos 11–12 days old, is dependent on the development and activity of the *plexus chorioidei*. A gradual widening of the brain then occurs in all parts of its cavity, in the *Aquaeductus Sylvii* as well as in the ventricles I–IV. The maximum degree of widening varies with age and individuality of the embryo. Characteristics of the anomaly are (*a*) the continued existence and sometimes even a considerable widening of the *Foramen anterius* ("Area membranacea" of Weed), which normally disappears with the development of the plexus; (*b*) a more or less accentuated reduction of the nervous tissues of met- and mes-encephalon along their medio-dorsal line, such nervous elements continuing, however, their development laterally. These characteristic features both bear witness to an augmentation of the fluid pressure within the brain. A further localization of the hydrocephalous effect is brought about at birth, when the third ventricle and the aqueduct are considerably narrowed under the pressure of the rapidly growing hemispheres as well as of the lateral parts of the cerebellum. The head of the young mouse assumes its characteristically swollen, ball-like appearance.

Early stages of this hereditary hydrocephaly are to be found in embryos 11 days old or younger which show normal development of the medullary tube, but an abnormal infiltration of fluid into the surrounding connective tissue. The excess fluid may escape from the posterior end of the medullary tube and even the epithelia of the open ear vesicles, but after the closure of these openings, in embryos 10–11 days old, a critical period of abnormal tension within the connective tissue follows which seems to last until the chorioid plexuses become active. This tension leads to frequent bleeding, and deformation or a real breakage of hemisphere walls. This critical period of the hydrocephalous development ends when the fluid escapes through the plexus into the brain cavity.

An abnormal fluid infiltration of the embryonic tissues has been observed as early as the stage of implantation of the embryo in the uterus. The possibility that in this mutation the recessive homozygotes might be represented not by the hydrocephalous individuals themselves but by their mothers has been tested by an outcross to normals. This proved that heterozygous F_1 females mated to a brother may produce hydrocephalous young. Clearly, the recessive tendency to fluid formation leading to hydrocephaly is due to the homozygous fertilized egg and not to the mother's uterus.

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BONNIER, G. ***Theoretical and Practical Possibilities of Genetics in Contributing to the Improvement of Livestock***

Twelve years ago, at the Genetics Congress in Berlin, Prof. Crew (1927) delivered an address about how a research institute for animal breeding should be organized and what its most important functions are. He was then discussing the institute in which we are guests to-day, and all of us who have followed the activities of this institute know that his programme was well conceived and has proved successful. Animal genetics is very much indebted to Prof. Crew and his collaborators. In speaking of the possibilities both theoretical and practical for the application of genetics to the improvement of livestock, my task to-day is to a certain extent the same as Prof. Crew's was in Berlin. The subject of my paper, however, concerns no special institute. But my own experience in the study of these problems comes from the work at the Swedish Animal Breeding Institute at Wiad. Thus any discussion that I make of these problems will be to a certain degree a review of the problems which are now under investigation there.

Animals differ from each other—they vary. The selection which is the chief problem of animal improvement involves choosing those animals for parents whose progeny will be the best possible. But the causes of the variation of animals are not always the same. By and large they can be attributed to differences in genotype or to differences in environment during development. *A priori* we seldom have the possibility of determining in any special case which of these two is the effective cause. But obviously selection can only be effective when the differences are genotypic. When the differences between animals are merely the result of differences in nourishment, selection will have no effect. These are all truisms. But they emphasize the great desirability for each kind of animal and for each character of making more precise the relation between heredity and environment. For only when this is known is it possible for us to tell what the effect of selection would be. There are a number of ways in which this problem may be attacked. The statistical method gives the best general survey. Thanks to the foundation for statistical studies in genetics which has been laid by the work of Prof. R. A. Fisher and Prof. Sewall Wright, it is now often possible in a given material to compute the proportion of the total variation resulting from hereditary causes. Such investigations have recently been made in different parts of the world. But what has been done up to the present can only be considered as a small beginning. It seems to me that the analysis by methods of this type of material after material will for some years to come occupy a great part of the attention of investigators of animal-breeding problems. At the present time there are not many analyses of this sort published. But of those which have appeared several show that the variation is to only a very slight extent hereditary in origin. For example, we have compared the milk yield of dams and daughters within quite a large number of herds in Sweden. After elimination of as much as possible of the non-hereditary variation an extremely small dam-daughter correlation is left, whereas the corresponding correlation between herds is considerably larger. This indicates thus a very strong environmental influence on the variability of milk yield. As a result of this kind of statistical analysis it is thus possible to have a much clearer view of the difficulties of the material with which we are working.

The statistical analysis, as I have already said, gives the best survey. But it cannot be so definite as an experiment. Especially in the study of the relations between heredity and environment in the size of yield, the study of individual cases under controlled environmental conditions would be of great importance. Of the different environmental factors which may act as causes of variation, feeding policy is in many cases the most significant. Feeding as such is not a genetical problem. But in the present con-

nexion it may be useful for the geneticist to add the study of the food as an environmental factor to the more strictly genetical problems. Rather comprehensive studies of this type have been carried out at Wiad. They have consisted mainly of studies of the effects of over-feeding, carried out in a number of different ways, having as their purpose the increase of milk production by means of a controlled rich diet. It would take me too far afield to go into the details of these experiments here: I can say, however, that the results were nearly completely negative—there was hardly any indication of an increase as a result of the extra food (Bonnier, 1935; Bonnier and Bäckström, 1935; Institutet för husdjursförädling, 1939). The conclusion is then justified, it would seem, that it is at least very difficult to achieve a perceptible increase in milk production by means of similar high feeding to that used in our experiments. But the statistical analyses that I have just mentioned showed that the environmental differences between different herds had a strong influence on the correlations for milk production between relatives. There would appear to be here a serious contradiction between the experiments, which show no effect of controlled changes of nourishment, and the statistical analyses, which show a clear influence of the environment, on the milk production of cattle. What the explanation is cannot be said at present. It is possible that, meaning by undernourishment a diet inadequate for their constitutional or hereditary demands, different degrees of undernourishment occur in the different herds. It is also possible, and I personally am more inclined to this point of view, that it is the food and other environmental differences during development (the growth period) that are significant for the future milk production. We have planned a programme of such experiments at our institute. The prosecution of researches of this type on problems of nutrition are not only, and not even primarily, important with respect to the problems of nutrition themselves: their greatest value lies in the opportunity they give to the animal geneticist of distinguishing the non-genetical causes of variation. For with this knowledge he also has more information about which part of the variation is genetically determined and in consequence is better equipped for his selection work.

The nutrition experiments that I have just spoken of suffer from a great weakness. Since exact comparisons are difficult to make, the results can often be interpreted in different ways. It is hence desirable to make them still more precise. This can indeed be done to a considerable extent, if one is prepared to decrease the number of experimental animals. For here monozygotic twins may be used for study. The members of such a pair of twins are genetically identical, hence experiments involving comparative nutrition or other environmental factors should give as clear evidence as can be imagined. There are two difficulties, however: to procure twins, and having procured them, to identify them as monozygotic. Identical twins, in domestic animals, do not unfortunately grow on every tree. According to the rather rough estimate that the statistics of calf births give us, 10 % of the twins of like sex born in Sweden are monozygotic, and $\frac{5}{10}$ % of all calvings are twin heifers. Thus about two thousand calvings are necessary to make it possible to obtain one single pair of monozygotic twin heifers. For this reason the Animal Breeding Institute has addressed itself to the owners of altogether more than 25,000 cows, offering to buy the twin heifers born in their herds. Since 90 % of these are expected to prove dizygotic on analysis, and must be sent to slaughter, it has not been possible for the institute to offer more than slaughter price for the twins, so that not all owners are willing to sell their twins to the institute. Also it not infrequently occurs that owners forget the institute's call or remember it after their twins have been sent to slaughter. At present, after $1\frac{1}{2}$ years' work, we have received only enough twins to yield one uncertain and five certain pairs of monozygotic heifer twins. We are now appealing to a still larger number of other herd owners, also calling again upon those previously addressed. It is our hope that in this way we shall eventually obtain about ten pairs of monozygotic twins per year. There are two main types of experiment that we have under way. One is the comparison of the effects of differences in nutrition between the members of a pair on their prospective milk yield; one of the twins is given a high percentage of concentrates, the other a low percentage, during their growth. In the other type of experiment, both members of the pair are identically treated until after the first lactation period. With the beginning of the first dry period, differences of feeding begin; in this way we hope to get more exact data on the so-called effect of the previous dry period. Up to the present none of our twins has begun to give milk, so that the results are not as yet available.

In all of these studies we aim at having the twins under our control as early as possible, at the latest when they are a few weeks old. This makes it necessary to have methods at hand for the recognition of monozygotic twins even in very young calves. In man the question is relatively simple: twins of the same sex, and strikingly like each other, are usually monozygotic. In calves also, the criteria of monozygosis must be based on similarity. But, owing to the standardization of breeds brought about by the efforts of the breeding associations, a striking likeness between the members of a pair is not enough. If one relied on this alone, he would find monozygotic twins almost everywhere. But owing to the extensive re-

searches of the late Prof. Kronacher (1932) of Berlin and his school we have now available methods for the identification of monozygotic twins in cattle. He did not, however, study new-born twins, so that many of the characteristics that he used (distance between horns, distance between certain protuberances on certain bones, and a number of other similar measurements) are either useless or very doubtful for small calves. At Wiad we now use three criteria: the form and position of the whorls of the hair, the nose-prints —two of Kronacher's criteria—and the microscopic structure of the different hair types as shown in cross-sections of the hair (Bonnier and Skårman, 1938). Taken together with the general impression given by careful examination of the appearance of the calves, these three characteristics suffice as criteria, in general. There are, however, many cases in which they leave an element of uncertainty. It would be of some importance therefore to have new criteria established, which would be valid for small calves, easy to determine and relatively little influenced by environmental factors such as nutrition or by changes in the state of health. The scope of these studies of identical twins is, as I have already said, limited by difficulty in procuring a sufficiently large material. But it seems that were such studies carried on in a number of laboratories, the results would give more information about the genetics of milk production than a very much larger number of experiments with feeding heterogeneous groups of animals.

In the foregoing I have touched upon a number of different problems under investigation at the Wiad Institute of general interest for the problems of animal improvement. Obviously many such problems could be added—the elimination of lethal genes from valuable breeds of swine; studies of the variation in calcium, the deficiency of which in the tarsal bones of certain boars from good breeds creates difficulties in their use as breeding animals; practical methods of measuring certain characteristics of wool; seasonal variations in egg weight in poultry, the study of which should make it possible to determine at what time of year the eggs should be taken as having the most characteristic weight for a breed of poultry; and studies of the physiological differences in case of fertilization in different hens—and so on, and so on. If, in addition, I should go on to consider the many important problems that are under study at other institutions, I could continue as long as desired. All studies adding to our knowledge of the heredity of domestic animals are of value, particularly when they have been subjected to a proper statistical analysis.

Yet, in evaluating the different studies, we are confronted by a serious problem. Everyone with the responsibility of directing research in an institution whose purpose is in any way practical knows what resistance he must make against the continuous cry after "results". Nevertheless, it must be recognized that, in answer to this cry, the presentation of a correlation coefficient is not far from giving stones when asked for bread. The problem before us is then what "results" really are, and to what extent can and ought we to attempt to achieve "results"? Personally, I think I know moderately well what people, especially in Sweden, mean—even though they have perhaps not formulated it clearly for themselves—when they ask for "results". For in Sweden the improvement of plants effected at Svalöv has become something that farmers are not only proud of, but from which they derive obvious benefit. For they know well how much greater their yields are from the seeds that are sent from Svalöv than from the old original stocks. By results then people mean something comparable to what has already been accomplished in the field of plant improvement. But what are the comparable things to be done by an animal breeding institute?

To answer this question one must go into the reasons for the extraordinary successes of the plant breeding institutions. It is certainly not necessary that I go into the history of how plant breeding developed and what it has accomplished. But I should like to stress a few important relations. Plant breeders have through selection and hybridization developed new types which give a greater return for the farmers' labour. But by itself the development of new types would have had no perceptible value for these people, had it not also been possible for the plant breeders to multiply the desirable types on such a scale that seed could be supplied to a practically unlimited number of farmers, and that not only for one but for a whole series of plant generations. What I wish to point out is that although the development of the new types was the primary necessity, the cause of the practical value of the results was that plant breeders were able to take care of each new variety and did not risk losing it after one generation or another. And through mass multiplication of the new types without any consequent change in their genetic composition, they were able to place them at the disposal of large numbers of farmers. The biology of animals is unfortunately such that we cannot directly copy the methods of the plant breeders in this respect. The animals with which we work have neither vegetative reproduction, they are neither self-fertilizing nor parthenogenetic, nor do they display the mass multiplication that is found among the cross-fertilizing plants. But, we may ask, can we not take such measures of technique and organization that we may be able to imitate the capabilities of plant breeding in certainly a modest but nevertheless a substantial way from the farmer's point of view? This question, of

course, strikes with especial force the workers in the central institutes of animal breeding.

A considerable part of animal breeding is carried out by the procedure of selecting young males with respect to their pedigree, and then mating them after some special system with a group of females as large in number as possible. It is obvious that an animal breeding institute with its much larger resources can work on the same principles with somewhat greater success than the individual animal breeder. For within an institute there are probably resources which enable a more careful and detailed study of the animal's productivity, and also by intra-familial and other types of breeding, make it possible to gather more desirable genes in the males produced for breeding. By the production of such males on a large scale and their sale to the private herds, there are certain possibilities of introducing into these herds a fair number of good productivity genes. But if we recall that the correlation between parent and offspring is often very small—and I may refer to the recent researches of Lush and Shultz (1938), showing how slight the pedigree promise of a bull is with respect to his daughter's yield—it must be admitted that although work of the sort just mentioned would certainly be helpful to the animal breeders, the results would not be very much greater than what the animal breeders get in any case. An evident improvement in our ability to judge the genetical value of an animal lies in the progeny test. In a number of countries, among which Sweden is included, progeny tests of the breeding boars are regularly carried out by the procedure of sending groups of their progeny to an official station, where they are fattened under constant conditions and are carefully examined after slaughter. And the practice is now growing, in Sweden, of judging the milk value of a bull by the yield of his daughters. Even though progeny tests are fraught with much uncertainty, I can see no prospect at present of a better method for the larger domestic animals. Nor can it be denied that there is value in selecting young males from the offspring of a sire with a high grade in progeny tests, especially in cases where the parent-offspring correlation is high for the characters in question. But in those cases where the correlation is low, should the selection of male offspring as breeding males be the only purpose of the progeny tests of the sires it would seem that much labour is wasted. For, since the further removed in the pedigree an ancestor is, the less is the value of this pedigree. And it is therefore clear that a good progeny test is put to better use by as extensive use as possible of the sires tested, for the production of milking daughters, than if they are only used for the selection of sons as breeding males. Particularly is this true in the case of milk yield, in which Dr Buchanan Smith (1937) has adduced evidence which strongly suggests that some of the important genes are sex-linked. In such cases the value of selecting breeding males from the progeny of a progeny-tested sire is diminished, since in mammals the males receive their *X*-chromosomes from their mothers. For these reasons it seems to me that the attempt must be to utilize as effectively as possible the bulls who have proved especially good in progeny tests. But how is this to be done? In general, before a given bull has sired enough daughters that have produced milk long enough to enable a judgement of his value, he has been slaughtered, or at the most is too old to produce very many more daughters. Here the recent advances in the technique of artificial insemination may be used to advantage.

At the Wiad Institute we have made arrangements with a number of neighbouring herd owners to take over the servicing of their herds. When a cow in one of these herds comes into heat, the herd owner telephones the institute, upon which one of the men in charge of that work goes there and the cow is inseminated with the bull sperm he has brought. In this way, due to the high dilution of sperm that can be used, one ejaculation will suffice for many cows. We calculate that after a bull has been used in this way for about half a year, there will be enough of his daughters produced to suffice for a progeny test. Therefore we are continually buying young bulls—about 1½ years old—chosen on the basis of their pedigree and of progeny tests of their ancestors, in the belief that they will be genetically valuable. More critical information concerning their value subsequently comes from their progeny tests. The bulls are thus used in this way for about half a year, and thereafter are kept in a suitable place pending the outcome of the progeny test. Progeny tests of such bulls are not as yet available, since it is only recently that our programme commenced; but we estimate that the tests will be in when the bull is about 6–7 years old. Consequently we have as yet not dealt with the problem of the intensive utilization of the bulls which have proved to be the best. We have, however, our own experience as well as that of other laboratories to guide us, for we know that this can be done with artificial insemination. Thus it should be possible for us to have those bulls whom we believe are the best, produce a large group of daughters in a large number of milk-producing herds. It is certainly not utopian to assume that a carefully planned organization of the utilization of these bulls in the manner described should result in a progeny of several thousand daughters per bull. What this may mean for the farmer and for the country is obvious.

That there are difficulties in the carrying through of the programme is clear. Some bulls die before

they can be used, others become sterile, and so on, But the greatest difficulty we have met is a psychological one: it takes some time before people accept as a regular practice the use of artificial insemination. From our point of view it would of course be best if the testing of the young bulls were done on our own herds, but unfortunately these are not sufficiently large. This would have another advantage could it be done. Progeny tests may be misleading where environmental influences are important. Were the tests made on our own herds progeny from the individual bulls could be separated into groups fed and treated in different ways, and in this way to a certain extent the environmental factor could be eliminated from the progeny test. This cannot at present be done. But, since the progeny tests of bulls are made in a number of different herds where the general environment is unlike but nevertheless can be graded by us, it is still possible to a certain extent to judge the effect of environmental variations, and thus to a certain extent eliminate them from the progeny tests, even though not as completely as if the herds were our own. As regards the psychological resistance I am convinced that it will give way as the advantages of the programme are more fully realized.

It would be of course an exaggeration to attempt to claim that work with domestic animals of the type I have outlined is strikingly similar to the working methods of the plant breeders. But it does combine, in a way, the best practical method of judgement—the progeny test—with one of the distinguishing characters of plant improvement, namely, the preservation of a valuable result—in our case the valuable bull—so long as possible once it is obtained, with its utilization for a large number of farmers.

With the smaller domestic animals, naturally enough, it is much easier to copy the technique of plant breeding than with the larger ones. Especially is this true of poultry. In this species it is known that, just as in many others, there is a strong manifestation of hybrid vigour. According to both our own experience and that of others, it is possible by suitable crosses to obtain hybrids which are very good layers and at the same time good for slaughter. For example, we have obtained from the cross of white Leghorn males by white Wyandotte females, F_1 animals considerably superior to both the parent races. The reciprocal cross does not give as good a result, which must, as far as I can see, depend upon the presence of important sex-linked genes. The better of the parent races should therefore be used as the male parent. But not all crosses of white Leghorns by white Wyandottes give good laying daughters; hybrid vigour may find its expression in fat or general well being. It is therefore necessary by selection and progeny testing to try out which animals of the pure races give especially good F_1 daughters. And such F_1 daughters we should like to produce in as great numbers as possible in order to distribute them to the many egg producers who either do not find it necessary or desirable to carry out their own breeding. This raises the question of the technique of such a mass multiplication. For on crossing cocks and hens of the different races, the parents are ordinarily 2–3 years old before their F_1 daughters have shown whether the combination of parents was successful. If one should subsequently desire to use these same parents for the production of large numbers of F_1 daughters for sale, the difficulties are obvious. But these difficulties can, I believe, be circumvented if the work is carried out with whole populations whose genetic structure is maintained constant so far as possible from one generation to the next. The situation here recalls to a certain extent that in the cross-fertilizing plants. In these plants, of which rye is an example, the possibility of maintaining the different varieties without any appreciable genetic change from generation to generation depends on the fact that all possible combinations of gametes occur, and that each test sample of seed is sufficiently large to be representative of the whole crop. The characteristic features then that in a plant like rye enable the sale of a kind of seed that has once proved valuable, over a number of generations, to a large population of farmers are (1) mass multiplication and (2) panmixis. As far as panmixis is concerned, that can easily be attained in animals by mixing sperm from many males and inseminating many females therewith. But just this "many"—the mass multiplication—makes the difficulty in animals. I have made some calculations of the changes in gene frequency that occur in these cases. The results show that by taking 100 animals of each sex at random out of a population, mixing the sperm of all the males and inseminating the females with mixed sperm, the genetic structure of the population is maintained appreciably constant for a few generations. This holds for all populations of pure races, and is not directly concerned with the production of F_1 animals. Since, however, these are the best egg-layers, the scheme we have adopted at Wiad for the practical work is the following: First the usual selections are made to obtain animals that give the best F_1 daughters on crossing. From these animals and their close relatives, populations are derived which are increased by the panmixis described. At the same time the crosses between the populations are carried out and the egg production of the daughters of the progeny gives the information needed concerning the suitability of the population. Since the genetic structure of the population remains practically constant from one generation to the next, the egg production in the F_1 animals born one or two

generations earlier can be taken as characteristic for the new F_1. Thus by breeding from populations one of the advantages of the plant breeders from the farmer's point of view has been attained, namely, a rather good prediction of the mean yield of the F_1 population. And the limitations of the extent of this kind of work are not breeding problems but problems of organization. Such work may be carried out on any scale desired.

In conclusion I should like to touch on another of the methods of plant improvement. Of recent years the production of polyploids has taken much of the attention of plant breeders. Polyploids in animals are rare, and it is hardly known that such can be obtained at all in vertebrates. But the importance of such a result is so evident that a serious attempt should be made. In plants the work of the last two years has shown that chromosome doubling can be achieved by the use of certain drugs (Dustin, 1934; Lits, 1934; Blakeslee and Avery, 1937; Nebel and Ruttle, 1938; Levan, 1938, 1939). A year ago therefore we began colchicine experiments with swine and poultry. The work thus far has concerned determination of dosage, etc., and there are no results as yet. To identify possible triploids in poultry, I have obtained from Prof. Warren in America a small number of animals heterozygous for the three linked genes: crest, dominant white and frizzle. The dominant genes are alternated, so that all three genes can only be found in the same individual from an outcross to the triple recessive if double crossover or if triploidy has occurred. According to the published data (Warren and Hutt, 1936) no double crossing-over occurs between these genes, and one has therefore a good check on the success of the colchicine experiments. Our work so far has been the multiplication of this stock, and it will not be before next year that definite experiments can be started. It seems to me very worth while for many workers to enter this field, and it would be very interesting to correlate the work in the different laboratories.

In the foregoing, using as examples the work we are carrying on at Wiad, I have reviewed a number of the genetical experiments which seem to me of importance if we are to work for the improvement of livestock. They were both theoretical and practical, but I have especially wanted to stress the practical aspects. This is not that I think the theoretical aspects less important. Theory is basic to practice, and aside from the purely scientific value that theoretical research has in itself, it is indispensable for the practical work. What I have wanted to do is to put the consideration of how best to apply the advances in theory, into the foreground. If we confine ourselves to telling the farmers what we find, leaving them to their own resources to apply this knowledge, the value of our work remains purely academic. As regards the work itself that is carried out in institutions of animal genetics, there must naturally be full freedom for the individual workers to follow their own interest in the field. Only so can one encourage good work. But I am convinced that institutions whose purpose is the production of improved breeds of animals cannot confine themselves to purely consultative work. They must—even if sometimes only in a limited way—be guided by the point of view that has in principle proved so valuable for plant improvement: it is for the farmer to say what kinds of animals he needs, but the central institutions, with their greater experience in most cases and always greater resources, should attempt themselves to produce or to organize the production of these animals or of their sires.

Summary

A number of different fields for investigations which are of importance for animal breeding institutions have been enumerated. In order to lay the selection work on a more stable ground studies on the part of variation due to environment are looked upon as especially important. Such studies may be attacked in different ways: by statistical inquiries, by planned feeding experiments, by studies of monozygotic twins.

Theoretical studies are basic to practical breeding work. But it is emphasized that if the knowledge that we gain is to be of practical importance for the farmers, the animal breeding institutions must engage themselves more directly in the production of the animals desired. Some methods to achieve these ends are discussed.

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33

BONSER, G.M. ***Presence of Brown Degeneration in the Adrenals of Mice of Several Strains***

It was shown that in untreated females great differences in degree of brown degeneration were found. The change was very marked in R III (high mammary cancer), fairly marked in white label (Kreyberg), slight or absent in Bagg albinos (high mammary cancer) and "market" females actually bearing mammary cancer, and completely absent in black agoutis (CBA) and IF mice (both low mammary cancer). In untreated males of all strains it was slight or absent.

In oestrogenized R III males or castrated females brown degeneration was very advanced. In similarly treated Bagg albino and black agouti (CBA) males it was slight or absent. In non-castrated oestrogenized black agouti females it was slight or absent.

It was pointed out that the R III strain seems to stand by itself in regard to its great tendency to develop advanced brown degeneration, and it was urged that more strains should be studied in greater detail before an aetiological relationship with the development of mammary cancer can be proved.

34

BONSER, G.M. ***The Effect of Genetic Constitution in Determining the Response of the Animal to Carcinogenic Agents***

It is well established that animal species vary very greatly in their manifestation of cancer and in their response to carcinogenic agents. Cancer in one species is not transmissible to another species. More recently a growing volume of evidence has accumulated from the study of pure lines which has shown that the genetic constitution of the animal is an important factor in determining its reaction to carcinogenic agents. The fundamental reasons for these differing responses are still largely unknown.

It is proposed only to bring forward some of the evidence which bears on two aspects of this subject: first, in relation to carcinogenic substances acting at the site of application, and secondly, in relation to those oestrogenic substances which act on tissues removed from the site of application, and which are associated with the development of mammary cancer.

(1) Carcinogenic agents such as tar or certain hydrocarbons may be applied to the skin or injected into the subcutaneous tissues. In the former case Kreyberg showed that of two strains of mice which he happened to have in his laboratory, one developed tar warts much earlier than the other. Bonser was able to establish a strain of mice by selective breeding in which benign and malignant tumours of the skin appeared specially early, and the characteristics of these mice will be described.

As a result of injection, genetic differences have also been demonstrated, notably by Andervont. There is no evidence that the tendency to develop spontaneous mammary tumours is in any way associated with an increased rate of induction of subcutaneous tumours by means of carcinogens, but there is some evidence that there is an inverse ratio between the susceptibility of the skin and of the subcutaneous tissues.

(2) It is accepted that there is a gradation of response by male mice to oestrogens, those of certain strains failing to develop mammary cancer while those of other strains develop a high incidence of this type of cancer. This gradation reflects the ability of the females to develop spontaneous mammary tumours, although when castrated females of high mammary cancer strains are treated with oestrogens their ability to develop mammary cancer is reduced. The possible mechanisms of these differences will be discussed.

35

BOYDEN, A.A. ***Genetics and Animal Relationship***

A critical examination of the principles of phylogeny from the viewpoint of modern genetics is long overdue. Of the generally accepted phylogenetic principles, four require genetic revaluation. These four may be briefly stated as follows:

(1) All animal relationship is genetic.

(2) Animal relationship is and should be determined chiefly by morphological comparison of fossils, and of adult and developmental stages of existing forms: the greater the similarity the greater the genetic relationship.

(3) The "central concept" of comparative morphology is that of homology, which is a fundamental similarity in the structure and development and in the relative position and connexions of corresponding organs or parts of the bodies of different organisms.

(4) The goal of taxonomy is the expression of phylogenetic relationships.

Principle (1) would be true only under the following conditions:

(*a*) Only hereditary traits are used in the determination of animal relationship.

(*b*) The origin of animal life was monophyletic.

(*c*) If animal life is polyphyletic no genetic relationship is implied between the descendants of different origins from non-living things.

Since the knowledge relating to inherited characters is inadequate in most phyla, and since we may never be able to decide between mono- and polyphyletic origins, it would be wiser to use the term "genetic relationship" with more caution hereafter.

Principle (2) should state clearly that only those morphological resemblances and differences which are conditioned mainly by inheritance can have genetic implications, and furthermore, that not only hereditary morphological but hereditary physiological characters should be used.

In recent years evidence has accumulated that such parts of the biochemic constitution as are best revealed by the precipitin reaction appear to have unusual values in systematic zoology. Thus, with an accurate and suitable method, the intensity of the interaction between antisera and antigens, such as serum proteins, parallels the systematic position of the species where that is well known. The facts indicate that the serological natures of animals are such that serum proteins must be conservatively inherited, and hence these data should rightly complement our morphological comparisons.

Principle (3) finds definite genetic confirmation, for the mechanism of heredity is the mechanism of homology. Every complex organ is conditioned by the interaction of many genes with themselves and with the cytoplasm, and this mechanism ensures that the essential agreements in adult and developmental structure and in relative position and connexions, which are so characteristic of homologous organs, shall be carefully preserved.

Principle (4) needs restatement. Where pedigrees are lacking, genetic relationship is inferred from similarity in hereditary traits. Classifications are never really "based on phylogeny", much less on genealogy; rather both classification and phylogeny are based on similarities and differences in the organisms compared. A truly "natural" classification can result from putting essentially like things together, and in expressing their likeness in terms of *animal relationship*. This is wiser than to abuse the concept of genetic relationship by insisting on applying it to animals of the most diverse kinds where proof of real genetic relationship can never be obtained.

36

BRIGGS, F.N. ***The Use of the Backcross in Plant Breeding***

In many cultivated crops there are numerous varieties, but comparatively few ever attain to any considerable importance. For example, there were 213 varieties of wheat in the United States in 1934. Three varieties, Turkey, Marquis and Blackhull, occupied almost 50 % of the total acreage. It is apparent that any new variety which finds an important place in the area occupied by these must have most of their favourable genes for yield and adaptation. Marquis attained its importance in the hard red spring wheat district in spite of one important weakness, namely, susceptibility to stem rust. Notable progress has been made in this region in breeding such rust-resistant varieties as Ceres, Thatcher, Apex and others. Marquis has been one of the parents in all cases. Whether or not these varieties will equal Marquis in its wide adaptation and high quality will not be known until they have been grown over the area for a number of years. The favourable gene complex of Marquis could have been kept intact by the use of the backcross and its susceptibility to stem rust corrected by the introduction of rust-resistant genes from the other parents in question. Such a breeding project could have been undertaken with certainty of success and with the knowledge that such an improved Marquis would be useful over a wide area.

The backcross method of breeding is based on the simple genetic fact that a heterozygous population backcrossed to either homozygous parent will become homozygous for the genotype of that parent. The proportion of homozygous individuals in any backcross generation will be equal to that resulting from an equal number of selfed generations. Because the character to be transferred from the non-recurrent parent must be maintained by selection, the backcross is most useful in the transfer of specific characters which can be followed accurately in hybrid generations. In cross-fertilized crops the most direct use will be to improve inbred lines. However, it should be pointed out that when the recurrent parent is heterozygous, the amount of homozygosity attained will never be greater than that resulting from one generation of inbreeding.

Our use of the backcross with cereals over a period of seventeen years and involving several projects will be of interest. In 1922, six commercial wheats were crossed with Martin for the purpose of transferring its bunt (*Tilletia tritici*) resistance to these varieties. After the sixth backcross seventy or more lines from each were bulked for the resistant variety. They have retained the name of the commercial parent to avoid any confusion among growers and millers who are

already familiar with their qualities. These varieties were released in 1937 and 1938. In 1930 seven other varieties were included in this project. These will be ready for commercial production in 1942, at which time bunt-resistant strains of all important California wheats will be available.

The incorporation of stem rust resistance in White Federation and Baart, our two most important varieties of wheat, was begun in 1930 using Hope as the resistant parent. Bunt-resistant strains of White Federation and Baart were used for the final backcross, thus combining resistance to the two diseases in these varieties. They were grown commercially in 1938.

In the most comprehensive project undertaken thus far we are incorporating resistance to bunt, stem rust and Hessian fly in Big Club and Poso wheats. A good deal of the work has been completed and these resistant varieties will be released in 1943.

37

BRUGGER, C. ***The Genetic Uniformity of Mental Deficiency without Marked Physical Signs***

The majority of mental defectives show no abnormality save retarded mental development. This group of uncomplicated cases of mental defect cannot be further classified by means of clinical methods. Some authors, however, suppose that several genetically independent types exist among these mental defectives. Stumpfl, basing his ideas on differences of character, has tried to classify them in several genetically different groups; but an independent hereditary transmission of these types has not yet been statistically demonstrated. The statistical investigations of Riedel disprove the hypothesis of genetic relation between defects of intelligence and character, and show that mental deficiency cannot be interpreted as a defect of character. Others suppose that mental deficiency may be due to recessive as well as dominant factors. A summary of all researches shows that their results correspond exceptionally well and prove a unified recessive determination. These investigations are based on 2380 sibs. The few deviating results which do not fit into recessive factors have been found in groups of only 5 and 32 sibs. The following facts contradict the assumption of dominant factors: 61·3 % of these 961 cases of mental deficiency, both of whose parents have been carefully examined, are the offspring of normally gifted parents. Cases of mental defect are no more numerous among the parents of feeble-minded than among those of imbeciles. 28·6 % of 342 parents of feeble-minded mental defectives, and 24·5 % of 676 parents of imbeciles. These results provide no reason for assuming that feeble-mindedness may be due to a dominant gene. All the researches, moreover, prove clearly that feeble-mindedness and imbecility in the majority of all families appear together. An independent inheritance of certain grades of mental deficiency has not yet been statistically proven. The feeble-minded are always much more numerous even among the relatives of imbeciles, specially among the parents. 19·6 % of the parents of imbeciles are feeble-minded and only 5·3 % imbecile. Similarly, 22·2 % of the parents of dulls are feeble-minded and 6·4 % imbecile. The results of different authors show that there exist no facts at present which contradict the genetic uniformity of all cases of clinically uncomplicated mental deficiency.

38

BURGEFF, H. ***Konstruktive Mutationen bei* Marchantia**

Europäische und tropische *Marchantia*-Arten sowie Artbastarde der letzteren mutieren in sehr verschiedener Richtungen. Ein Teil der Mutationen erzeugt Merkmale, die für andere Gattungen der Marchantiaceen charakteristisch sind und die Wege aufzeigen, auf denen sich die Marchantiaceen entwickelt haben. Einige andere Mutationsrichtungen könnte man als Neuerwerb deuten, so die aus Dichotomie in der "Vertikalen" entstehenden radiären Blastome der mut. *blastophora*, die Pflanzen von völlig neuem Typus erzeugen. Sie entbehren jedoch mancher notwendigen Differenzierung und sind als "Fehlkonstruktionen" ohne neue Mutationen nicht konkurrenzfähig.

39

BURKS, BARBARA S. ***Autosomal Linkage in Man***

The writer has secured some positive results on autosomal linkage through use of the method of like and unlike sibling pairs. Following a clue from Beadle's 1925 pedigree on congenital tooth deficiency and hair colour, the investigator used first fifteen pedigrees on tooth deficiency (together with other traits) available at the Eugenics Record Office, and then visited and secured field data from fourteen families located through clinics by X-ray diagnosis of congenitally missing teeth. Only subjects over 15 years of age enter the tabulations. The χ^2 test applied to fourfold tables of sibling concordance and discordance in tooth deficiency and hair colour showed the chances in the absence of linkage of results as favourable or more favourable to a linkage hypothesis to be approximately 0·10 for the E.R.O. data and 0·025 for the field data. Taking these results together with

Beadle's three-generation pedigree in which linkage seemed to be operative, we are left little doubt as to the presence of linkage.

Contrary to the belief of various dental experts, congenitally missing third molars are attributable to the same factor determining missing incisors and premolars. This was demonstrated through the linkage relationship of missing third molars to hair colour, and through other analyses of familial incidence of various locations of tooth deficiency. The deficiencies are distributed irregularly in the jaws of affected persons in much the same manner as missing bristles in *Drosophila* in the presence of the genes Dichaete, Hairless, Scute, or Echinus. It is probable that in at least some pedigrees missing third molars represent a simplex condition and missing anterior teeth a duplex condition. The recombination ratio (tooth deficiency and hair colour) is estimated as approximately 0·10.

Though "peg" or "rice" teeth often occur in families having congenitally missing teeth as genetic equivalents, the relationship of well-formed, but slightly undersized, teeth to the other tooth anomalies is not clear. The investigator recently studied all sibling pairs (age 14½ or more, of the white race) available in a secondary school population with respect to size of upper lateral incisors and other traits. Undersized lateral incisors, which occurred with high incidence, appeared to be linked to hair colour. Further study should indicate whether the trait is allelomorphic to deficiency in number of anterior teeth, or whether it is a simplex expression of the same gene.

40

CAMARA, A. ***The Effect of X-radiation on the Chromosomes of*** **Aloë arborescens**

The aims of this study are chiefly: (1) to find out whether there are critical regions in the chromosomes where ruptures occur more frequently; (2) to ascertain in terms of a ratio the relation between X-ray intensity and breakage frequency; and (3) to collect data for analysis of the mechanism of translocations.

Flower-buds of *Aloë arborescens* were treated by X-rays with intensities ranging from 100 to 700 r., with 65 kV., 5 mA., the apparatus being fitted with a filter 1 mm. thick, placed at a distance of 13·5 mm. For other material a different wave-length was used.

As regards point (1) measurements were carried out on fragments located near the anaphasic bridges. These measurements showed similarity in size of a great number of fragments in many cells where fusions of "chromatids" and related production of fragments were taking place. This suggests that parts of greater susceptibility exist in the chromosomes so that ruptures preferably occur at definite places in them.

Point (2) was dealt with by the studies in anaphases and counts of anomalies occurring in cells treated by X-rays in the early prophase. It became evident that there was a definite lack of linear proportionality in the relation between X-ray intensity and percentage breakage. Further extensive experiments in which the experimental factors were carefully controlled showed deviation from a straight line, thus agreeing with the results arrived at by Bauer, Demerec and Kaufmann. On changing the wave-length, however, but keeping the same degree as that under which the deviation had been noted, a decrease in the deviation was found, until the latter disappeared altogether at one of the above points observed. The invariable occurrence of this state of affairs suggests that the X-rays themselves are responsible for the lack of linear proportionality in question, and that it cannot be attributed to the influence of any controlled factor.

Regarding point (3) a certain amount of information was collected which affords evidence that translocations arise as a consequence of breakages followed by fusions. It appears that the latter can be accomplished without the chromosomes being in contact or adjoining. This assumption is based on observations of long slender and flexuous bridges which can sometimes be seen connecting the chromosomes during "pachytene".

The existence of such connexions lends support to the idea that under the action of X-rays a "chromatid" is caused to break and be driven away from its homologue, presumably due to alterations on the molecules close to the place of rupture. Under such circumstances the "chromatid" moves away until it attaches itself to another which has likewise undergone breakage. Also bridges were observed connecting two points of the same "chromatid". Many small inversions, translocations and deficiencies may be explained in the light of this mechanism.

41

CARIDROIT, F. ***Phénomènes d'hérédité liée au sexe: d'hérédité contrôlée par l'hormone testiculaire et de "crossing-over" dans les croisements entre les races Sebright Doré et Sebright Argenté***

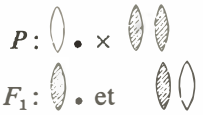
La race naine Bantam Sebright est remarquable par le plumage du Coq qui a les caractères de celui de la Poule. La castration établit que cette propriété est sous la dépendance du testicule. Il existe deux variétés Sebright: l'une, à plumes blanches lisérées de noir, est dite "argentée" (*A*); l'autre, à plumes jaune foncé lisérées de noir, est dite "dorée" (*D*).

Hérédité liée au sexe

Depuis longtemps, on sait que le croisement ♀ *A* × ♂ *D* et le croisement inverse ♀ *D* × ♂ *A* donnent des Poules-filles qui sont de la race du père. Les croisements de retour montrent qu'elles se comportent comme des animaux de race pure; leur ovariectomie confirme ce fait.

Nous pouvons représenter ces croisements par les schémas chromosomiques suivants:

I. Croisement: ♀ *A* × ♂ *D*



II. Croisement: ♀ *D* × ♂ *A*

Hérédité contrôlée par l'hormone testiculaire

Les Coqs issus des croisements précédents et correspondants au schéma , sont entièrement argentés sauf quelques-uns qui ont 3 ou 4 plumes avec un peu de doré. Le caractère argenté est donc *dominant* et le doré est *récessif*. La castration donne des chapons qui ont tous du doré occupant une place aussi importante que les surfaces restées blanches. *Donc le testicule contrôlait la dominance argentée.*

Des injections de propionate de testostérone faites à ces chapons font disparaître le caractère doré. Il n'est sensible qu'à une dose assez forte; sur l'un des animaux, 1 mg. par jour donne une féminisation totale et produit la disparition totale du doré; 100γ par jour, féminisation totale et encore un peu de doré; 50γ par jour, féminisation partielle et beaucoup de doré. Les sensibilités varient avec les individus, nous avons trouvé un échelonnement allant de 100 à 500γ par jour.

La même féminisation est obtenue avec le benzoate d'œstradiol mais la sensibilité plus constante (3γ par jour) montre que la bisexualité des hormones est surtout une propriété du récepteur.

Crossing-over

Les faits

1. Le croisement

♀ *A* × ♂ (*AD*)

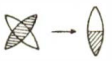
nous a donné des femelles argentées, des femelles dorées et une femelle "*crème*" (dorée excessivement pâle).

2. La Poule "crème" est croisée avec un Coq doré pur. Nous n'obtenons que des Coqs et des Poules franchement dorés.

3. Un Coq doré du croisement no. 2 est croisé avec des Poules dorées pures, nous obtenons une Poule "crème".

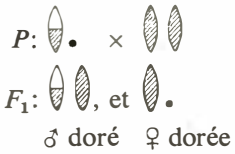
Interprétation chromosomique

1. Lors du croisement ♀ *A* × ♂ (*AD*), il y aurait eu "crossing-over"

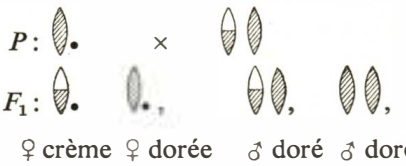


et la Poule crème aurait l'équipement .

2. Croisement Poule crème × Coq doré.



3. Croisement des Poules dorées pures avec un Coq doré précédent.



Conclusion

L'hypothèse du "crossing-over" rend bien compte des faits; nous devons donc obtenir des Coqs homozygotes pour le caractère "crème" en croisant les femelles "crème" avec le Coq doré du croisement 2.

42

Carothers, E. Eleanor. ***Interspecific Grasshopper Hybrids*** **(Trimerotropis citrina × T. maritima;** ***F_1, F_2 and backcrosses*****)**

As at present constituted *Trimerotropis* is the largest genus, in numberof species, of the Oedipodinae. For 25 years I have studied these various species both in the field and in the laboratory. Most of them are easily recognized, but races occur which seem to be intergrades of what in other regions are regarded as distinct species. The present work deals with such a condition. The species involved are *T. maritima*, essentially an Atlantic coast form found on sandy beaches and dunes from Maine (Morse) to Florida (Rehn and Hebard), and *T. citrina*, which extends along sandy rivers from Nebraska to the Gulf of Mexico and from Colorado to Virginia. The race,

T. Maritima interior, was described by Walker (1898) from the north shores of Lake Erie and Lake Ontario as having wing bands uniformly broad and dense black. Hubbell (1929) reported specimens from the southern shore of Lake Michigan as quite variable, the wing band being narrower than that of Walker's specimens and sometimes interrupted. Occasional specimens were scarcely separable from the Atlantic coast form. Rehn has called similar material from Iowa atypical *citrina*. The tegmina are banded, the wing bands variable, and the hind tibia either lemon yellow or coral red.

A genetical study was undertaken to determine the hereditary behaviour of contrasting pairs of characters and if possible to reconstitute the above-mentioned race in the laboratory. Parent stocks were collected near the centre of their respective ranges; *T. maritima* from the sand-dunes of Cape Cod and *T. citrina* from Kingman, Kansas. Both species are remarkably constant in their characteristics in these regions. Characters studied are markings of tegmina, width and extent of wing band, and colour of hind tibia. In *T. maritima*, tegmina are isabelline from posterior margin to cubital vein; anterior half with three triangular groups of loose maculations. Wings have a narrow black band, 3½ mm. in ♀♀ and 2¾ mm. in ♂♂, at its widest part, which extends caudad less than half the width of the wing. Costal margin and vein are yellow with band interrupted at first anal vein. Hind tibia is lemon yellow. In *T. citrina*, tegmina have three complete bands of fuscous maculations. Wings have wide black bands, 7 mm. in both sexes, which include costal margin and costal and first anal veins and extend to anal border. Hind tibia are coral red.

F_1 showed marked heterosis; F_2 were much less vigorous with poor viability (twenty-one reared to adults). Backcrosses were fully fertile and vigorous. While the work is still in progress the following summary may be given:

(1) Tegminal bands are dominant in ♂♂ and partially dominant in ♀♀.

(2) Width of wing band is intermediate in F_1, 5 mm. in ♀♀ and 4¾ mm. in ♂♂. Yellow costal margin and vein and first anal vein are dominant over black. Caudad extension of band to anal margin is dominant over shorter band of *maritima*. If these wing characters are due to different genes they are closely linked since they have not segregated.

(3) Coral hind tibia is completely dominant over yellow in ♂♂; partially dominant in ♀♀.

(4) All possible recombinations have been obtained in ratios which indicate that the genes for these characters are non-sex-linked and in different euchromosomes.

(5) All combinations reported for *T. maritima interior* have been obtained in the laboratory.

43

CASPERSSON, T. *On the Role of the Nucleic Acids in the Cell*

The substances belonging to the nucleotide group have a pronounced absorption band in the middle ultra-violet which can be used for the study of their distribution in the cell with optical methods.

In the *nucleus* the nucleic acids seem to be indispensable for the development of the chromosomes, and during the development of these structures they are specifically localized in the chromatids. Measurements during the meiotic prophase (grasshopper species) showed that the synthesis was completed before the tetrad split could be observed and before the main chromatid contraction had begun. It seems probable that the function of the nucleic acids of the chromosomes is especially connected with the gene division, and possibly with the subsequent chromosome contraction.

Dr J. Schultz and I have studied the metabolism of the *cytoplasm*. Their nucleic acids of different kinds can appear, with rare exceptions they are of the ribose type. In cells with a high growth potency, e.g. imaginal cells of the *Drosophila* embryo, the plant embryo, latent or manifest, the cytoplasms generally contain pentose nucleotids in high concentrations. The conditions are similar in cells which grow very rapidly without dividing. Several functions of the cytoplasmic nucleotides are probable: e.g. (1) to be reserve material for following nuclear divisions, (2) to be catalysts in the different metabolic processes in the cell or precursors to such catalysts, (3) to have a role in the process of the augmentation of the protoplasmic substances, most likely of the proteins. The last point seems to be of special importance.

The augmentation of nucleic acids on the chromosomes at the time for the reproduction of the genes stresses the analogy between the gene and the viruses and phages, which also contain appreciable amounts of nucleic acids in their molecules. It seems thus to be characteristic of self-reproducing substances to have nucleic acids in their molecules, at least during the time of their reproduction.

The cytoplasmic nucleotids are influenced by the genetical constitution of the nucleus, especially by a certain group of genes, as Dr Schultz will discuss in his paper. There is evidence that their actual synthesis occurs at the nuclear membrane. On the other hand, at certain stages the cytoplasmic nucleic acids influence the intranuclear ones and also the behaviour of the genes.

Thus the nucleic acids of the cell seem to be of importance not only for the energy metabolism of the cell but also for the increase of substances both in cell nucleus and cytoplasm. Apparently the nucleus is a

centre for the synthesis of the nucleic acids that s intimately connected with both the reproduction and the activity of the genes. In the typical cases the synthesis outside the nuclear membrane goes to pentose acids and inside mainly to desoxipentose nucleic acids.

44

CATCHESIDE, D.G. ***The Mechanism of Radiation-induced Chromosome Rearrangements***

Three major problems relating to the mechanism of induced structural change await solution. First, what is the nature of the physical energy necessary for chromosome breakage and recombination? Is it absorption of quanta, the passage of electrons or ionizations? Secondly, do the two or more breaks concerned in the production of a structural change have independent origins or a related one? This is the problem that is implied in the hypotheses of breakage and contact respectively. Thirdly, how long does the power for reunion of broken ends persist.

The solution of these problems must depend principally on the use of quantitative evidence. These are of four kinds: (1) the effect of dosage, (2) the effect of intensity, (3) the effect of wave-length, and (4) the frequency relations of various kinds of structural changes.

Previous work, mainly by methods (1) and (4), has led to the conclusion that either the contact hypothesis or a modification of the breakage hypothesis will account for the origin of structural changes needing a minimum of two breaks. It is possible that both mechanisms are responsible to different degrees.

New data suggest that the intensity at which a given dose of a given radiation is administered does influence the amount of structural change induced, though not greatly. This means either that the separate break mechanism rarely operates, or that broken ends retain the property of reunion for a long period. The latter possibility seems unlikely, for union between fragments produced separately in separate nuclei have not so far been detected.

Long-wave radiation, such as ultra-violet, induces very few reciprocal changes. Evidently, the low energy of ultra-violet quanta is usually insufficient to fracture more than one chromosome, but occasionally two breaks may coincide sufficiently in time and space to permit a structural rearrangement.

We may conclude that both contact and separate breakage mechanisms may be responsible, but that the former operates much more frequently.

45

CAVAZZA, F. ***Alcune osservazioni sull' ibridismo interspecifico dei Mammiferi***

Dopo avere accennato a precedenti suoi lavori su alcuni casi di fecondità accidentale di ibridi normalmente sterili tanto in Mammiferi che in Uccelli, l' autore parla dei caratteri somatici degli ibridi nati dalla unione di mula feconda con cavallo o con asino e quindi di quelli dei prodotti di seconda e terza generazione. Fa osservare che i figli di mula con cavallo presentano solo caratteri cavallini come pure tutti i discendenti da questi ibridi nelle successive generazioni.

Negli uccelli ha potuto osservare un caso accidentale di fecondità di un maschio ibrido figlio di un maschio *Anas platyrhyncha* e femmina *Cairina moschata*. In questo caso gli ibridi presentarono solo i caratteri di *Anas platyrhyncha*.

Viene a parlare dell' incrocio fra maschio di pecora con femmina di capra, citando il recente lavoro di R. O. Berry e dice che già cinque anni or sono il Dott. Ducros di Tripoli aveva ottenuti embrioni da tale accopiamenti uno dei quali in istato già assai avanzato. Ma tutte le femmine abortirono.

Volle provare pertanto la fecondazione artificiale che fu praticata dal Prof. I. Peli dell' Università di Bologna e le capre rimasero tutte incinte, ma abortirono anch' esse con embrioni di stato più o meno avanzato.

Chiude con considerazioni di indole generale accennando alle diverse ipotesi che possono spiegare: (1) Il fatto del ritorno a tutti i caratteri di una delle specie parentali; (2) Il fatto del non giungere mai certi embrioni al termine della loro formazione.

46

CHARLES, ENID. ***Contemporary Trends in Differential Fertility***

Comparatively few measurements of differential fertility rates come up to the standard of accuracy demanded by modern demographical research. There is, however, a considerable body of evidence to indicate that the decline in the birth-rate began in the higher income groups, and that at the end of the nineteenth and the beginning of the twentieth centuries there was a striking difference between poorer and richer income groups. Other differentials between social groups have been repeatedly observed. The urban-rural differential tends to lose its import-

ance in highly industrialized countries. Occupational fertility differences (e.g. miners, textile workers) are perhaps more persistent. There is clear evidence that these differences are tending to disappear as reproduction rates fall below the survival minimum. While they still persist they may provide information about what type of environment is compatible both with a high standard of life and with survival. The task of dealing with any genetic consequences which may have resulted from the differentials which existed at the beginning of this century are insignificant in comparison with the task of devising incentives to ensure that any considerable section of the population will maintain its numbers.

47

CHEVAIS, S. ***Contribution à l'étude du développement de l'œil du "mutant" Bar de*** **Drosophila melanogaster**

Il a été montré par Ephrussi, Khouvine et Chevais que des extraits de larves de *Calliphora* provoquent une augmentation du nombre des facettes des yeux des mouches portant la "mutation" Bar, quand on élève les larves sur un milieu contenant cet extrait. Ces premières expériences, où le nombre des facettes semblait proportionnel à la concentration de l'extrait, ont suggéré la présence, dans l'extrait, d'une "substance morphogénétique formatrice des facettes".

La présente communication apporte des nouvelles données sur ce phénomène, spécialement en ce qui concerne: (*a*) la période sensible, c'est-à-dire pendant laquelle l'administration des extraits est efficace; (*b*) le relation entre la concentration des extraits et le nombre des facettes.

Il existe une période sensible pendant laquelle l'extrait agit en augmentant plus ou moins le nombre des facettes suivant qu'une plus ou moins grande partie de cette période est couverte; elle commence 40 heures après l'éclosion de la larve élevée à 25° C. et se termine entre 60 et 70 heures. Si l'extrait est administré avant le début de la période sensible, l'augmentation est plus faible, et des larves élevées durant toute leur vie sur de l'extrait ne montrent qu'une petite augmentation. La signification de ces faits est discutée.

La concentration des milieux nutritifs en extrait influe aussi sur le nombre des facettes et celui-ci est d'autant plus grand que la concentration est plus forte. Le nombre des facettes croît plus vite que la concentration. Le nombre maximum de facettes obtenu jusqu'ici est de 500.

48

CHILD, G.P. ***The Effect of Increasing Time of Development at Constant Temperature on the Wing Size of "Vestigial" of*** **Drosophila melanogaster**

The time of development of an isogenic vestigial stock of *Drosophila melanogaster* was increased by two methods: (1) by adding Nipagin (ethyl-para-hydroxybenzoate) to the food, and (2) by adding only very little yeast to the food. Both methods are essentially the same in that the developing larvae are under starvation conditions. In a preliminary experiment 0·05, 0·1, 0·2 and 0·4 % Nipagin were used. With increasing concentration there was an increase in the time of development and increase in the size of the wings, males showing a greater effect than females. The large wings resembled those of other vestigial alleles raised under normal conditions. The mortality was very high in the 0·4 % Nipagin.

In another series of experiments 0·1 % Nipagin and starvation were used. The larvae were removed from the culture as they pupated, to determine the relation between time of pupation and wing size. The first flies to pupate did not differ significantly in wing size from controls at that temperature. With increasing time of development there was an increase in wing size. Larvae which were much delayed, however, developed into small flies with small wings. These wings, although small, were more differentiated and larger than the control wings.

The "carry-over" effect was studied using normal food. The treated females and males were mated with control males and females respectively. Treated males were also mated with treated females. The wings of flies from this latter mating showed the greatest carry-over effect. Treated females by control males resulted in flies having a significantly larger wing size than flies from the reciprocal cross. These results indicate that there is a definite effect on the eggs and sperm of flies raised under starvation conditions, which effect shows itself in the subsequent development of the eggs and sperm.

49

CHILD, G.P., BLANC, R. and PLOUGH, H.H. ***The Effects of High Temperature on the Development of Heterozygous Recessives of*** **Drosophila melanogaster**

Larvae and pupae of *Drosophila melanogaster* were exposed to 36·5° for 12 hr. during different periods of development. The stocks used were wild type and heterozygous 1-ple, 2-ple, and 3-ple. A number of the characters of the heated flies showed the partial or

complete expression of the recessive genes. The degree of this incomplete dominance was more or less specific for the time of heating, in fact a few of the characters of the heated flies were more influenced by the time of heating than by the genotypic constitution. These results will be shown on a series of charts.

The dumpy gene was selected for special study and was introduced into an isogenic wild-type stock. High temperature during the first day of pupal life was found to alter the expression of the character in both heterozygous dumpy and wild-type cultures. Carefully timed pupae were subjected to 36·5° for 6–12 hr. at definite periods after they had pupated. The results showed that the sensitive period for the dumpy reaction begins earlier in the females than in the males, 10 and 13 hr. after pupation respectively. The effect in the males, however, is much more pronounced.

In general, flies are fairly uniform under most environmental conditions under which they will develop to maturity at all. However, it is well known that small differences in body size and colour, eye size, wing length, etc., appear in wild-type and heterozygous recessive stocks raised at different temperatures. This behaviour has been interpreted in terms of the rate theory as that of a complex reaction system in which the temperature coefficients of the various reactions are not necessarily equal but at least in harmony with one another within the range of temperatures in which the flies develop in nature, thus producing a fairly uniform phenotype under various "normal" conditions.

The short exposures of the wild-type and the heterozygous recessives to 36·5° at specific periods during development may have a differential effect on the reactions going on at that time. The slight differences in the temperature coefficients of the different developmental reactions would produce a much greater effect on rates at the elevated temperature, and thus the phenotypes would be greatly affected. The fact that the same kinds of specific effects were produced in the wild type and in the heterozygotes, but to a greater extent in the latter, supports the hypothesis that the same reactions were taking place but at somewhat different rates and with different temperature coefficients.

50

CHRISTOFF, M. ***Polyploidy and Apomictic Development in the Genus*** **Potentilla**

The caryological study of some species of the genus *Potentilla* demonstrated that polymorphism in this genus is accompanied by a large series of polyploids.

In some of the species, however, forms were found within the same species which differed in their chromosome numbers. The odd chromosome number of some of these forms indicated that hybridization was significant in the evolution of the genus. This also is to be presumed from the intermediate appearance of some of the forms with odd chromosome number in the somatic cells of their root tips. In agreement with such a point of view comes the observation that meiosis in these forms is irregular, as it is characteristic of species hybrids.

On the other hand, hybrids obtained experimentally by crossing with each other species which propagate sexually are completely sterile, while forms which exhibited an irregular meiosis bred true, because of their apomictic development.

Studies on the embryonic development of such plants demonstrated that apomixis in *Potentilla* is due to nucellar embryony. The hybridization experiments showed that the crosses, reciprocally made, between species of which one propagates sexually and the other apomictically, produced uniform female-like progenies when the apomictic parent was pollinated by a sexual one, while in cases where those sexually propagating were used as female they exhibited a segregation when pollinated by the apomictic.

Since the apomictically propagated species, owing to disturbances in the meiosis, produce aberrant gametes, we observe that in cases where they are used in the crosses as pollinators to the sexual species, the progenies differ in their morphological appearance.

The peculiar behaviour of apomixis in some Potentillas is perhaps responsible for the fact that species hybrids stabilize as constant-propagating forms, and this enlarges the polyploidy and the polymorphism in the genus *Potentilla*.

51

CLAUSSEN, F. ***Zur Phänogenese von Missbildungen***

In der Erbbiologie vom Menschen erhält die phänogenetische Arbeitsrichtung besondere Bedeutung, weil seine Anatomie, Physiologie und Klinik am besten durchforscht sind und weil die eugenische Auswertung dringlich ist. In welchen phänisch verschiedenen Krankheiten kann ein bestimmtes Gen sich ausdrücken und wie bewirkt es sie? Die Klärung ist auch nötig als Vorarbeit für die weitere Genanalyse. So hat die variable Genmanifestierung besonderes Interesse, und als Methode die Zwillingsforschung, die Galtons Genie angebahnt und die in Deutschland Siemens, O. v. Verschuer und Luxenburger ausgebaut haben.

Ich möchte eine kleine Kasuistik über genbedingte

Störungen der embryonalen Entwicklung des Herzens vorlegen.

I. 6jährige eineiige Zwillingsschwestern. Bei II war ein angeborener Herzfehler schweren Grades bekannt, offener ductus Botalli; ausserdem Klippel-Feilsches Syndrom. I. erscheint normal, hat aber doch einen sicher krankhaften und angeborenen Herzbefund, wahrscheinlich ebenfalls ein Persistieren des ductus Botalli, nur in viel geringerem Grade. Aus der Familie ist nichts bekannt. Dieses Paar zeigt also quantitativ sehr verschiedene, aber qualitativ gleiche Manifestation.

II. 36jährige eineiige Zwillingsschwestern, die nach klinischer Analyse (mit Kymogramm und Elektrokardiogramm) übereinstimmend einen angeborenen Herzfehler haben, eine Stenose der Aorta, wahrscheinlich des Isthmus. Der Befund ist im ganzen gering, bei II etwas ausgeprägter als bei I. Paarling I hatte nur eine Schwangerschaft; die 14jährige Tochter hat auch einen angeborenen Herzfehler, eine schwere typische Pulmonalstenose, wahrscheinlich mit einem Defekt im Ventrikelseptum; sie ist debil, zeigt grossen Augenabstand und beiderseits Epicanthus. Paarling II hatte zweimal Abortus, zuerst von Drillingen im 6. Monat, dann von einer längst abgestorbenen Frucht im 7. Monat. Die Mutter der Zwillinge hatte 8 weitere Schwangerschaften; 2 endeten durch Abort im 2. und 4. Monat; 2 machten schwere Zangengeburten nötig, das eine Kind war zu gross, es kam tot, das andere starb nach 4 Monaten an Pylorusstenose; 1 Kind starb nach 3 Wochen, es war "im Kopf nicht ausgewachsen".

Bei diesem Paar ist also der Ausdruck des Gens am Herzen der gleiche und sehr geringe; bei der Tochter von I aber anders und viel schwerer; und vielleicht ist dasselbe Gen an den Totgeburten in der Familie schuld.

III. 28jährige erbgleiche Zwillingsbrüder. Sie haben ziemlich geringe Herzbeschwerden, aber beide doch einen sicher nachweisbaren angeborenen Herzfehler, wahrscheinlich einen Defekt im Ventrikelseptum, der bei I sich etwas schwerer auswirkt und mehr das rechte Herz belastet, bei II mehr das linke. 2. haben beide eine endogene Hypoplasie der Hoden (mit Sterilität, ohne abnormen Körperbau), die bei I die Grösse einer kleinen Bohne haben, bei II die Grösse eines Pflaumenkerns. 3. hat I eine Lippen-Kiefer-Gaumen-Spalte. II erscheint unbehaftet; aber sein 2. Schneidezahn oben links (der bei I infolge der Spalte garnicht entwickelt wurde) ist merklich kümmerlicher als rechts, kürzer, schmäler und konisch zugespitzt.

Nach dem, was man über solche Kümmerzähne im Spaltengebiet weiss, ist dies wahrscheinlich die geringste Manifestation des Gens, das bei I die Schliessung der embryonalen Spalte ganz verhinderte. Die gleichsinnige Abstufung im Grade aller drei konkordanten Anomalien legt nahe, sie alle auf dasselbe Gen zurückzuführen. Seine Manifestierung kann in solchem Grade labil sein, selbst wenn dazu Unterschiede im übrigen Genbestand nicht beitragen. Der Wirkungsbereich des Gens geht über die Hemmung des Gesichtsspaltenschlusses weit hinaus, es hat hier auch die Abteilung der Strombahnen im Herzen gehemmt und das Wachstum der Keimdrüsenanlage. Aus der Familie der Zwillinge ist nur bekannt, dass ein Muttersbruder eine Gaumenspalte hatte.

IV. 29jährige eineiige Zwillingsschwestern. Am Herzen konnte ich bei ihnen keine Störung nachweisen. II hat eine angeborene Spalte des harten und weichen Gaumens, I nicht. Aber die gesunde I hat einen Jungen geboren, der eine schwere Blausucht infolge eines Herzfehlers hatte und am 2. Tage starb; sein Gaumen war normal; an seiner linken Hand war der Daumen im Endglied verdoppelt. II hat eine normale Tochter. Aus der Familie ist nur zu erfahren, dass bei der Mutter des Vaters der Zwillinge unter 11 Schwangerschaften mehrere mit Frühgeburt endeten.

Die Fälle ergeben: Man muss bei gewissen in der frühen Embryonalentwicklung manifestierenden Genstörungen mit ausserordentlicher Entwicklungslabilität rechnen. Ihre phänische Auswirkung kann quantitativ und qualitativ sehr verschieden sein. Möglicherweise geht ein Teil der hier in den Familien der Zwillinge vermerkten Aborte und Totgeburten jeweils auf dasselbe Gen zurück, das sich in den angeborenen Herzfehlern und den Gesichtsspalten der Zwillinge äusserte. Erst, wenn man über solche Zusammenhänge mehr weiss, wird auch die Genanalyse beim Menschen fortschreiten.

52

CLELAND, R.E. *Analysis of Wild American Races of* Oenothera (Onagra)

In most organisms, the genes are arranged in a definite order in the chromosomes, the order being fairly constant within a given species. But different species of a genus may, and often do have different arrangements. By analysing members of related races from the standpoint of the differences which they exhibit in gene arrangement, some idea can be obtained with regard to the closeness of their relationships. In *Onagra*, profound rearrangements in the chromosomal material have been of relatively frequent occurrence during recent evolutionary development. The present study is part of an attempt to analyse the rearrangements which have taken place and to compare the various races from the standpoint of similarity in chromosome structure in order thus

to arrive at an understanding of the evolutionary history of a group which has been the despair of the taxonomists. This study is based upon the assumption, for which much evidence exists, that similarity in the arrangement of chromosomal segments is an indication of recent common ancestry. A progress report is presented indicating the degree to which the analysis of segmental arrangements in the various wild genoms has been carried, and some of the phylogenetic and other implications of those findings are discussed.

53

CLEMENTE, L.S. ***The Lethal Effect of the Combined Purple and Eyeless Genes in*** **Drosophila**

It is shown that the double recessive purple eyeless is a zygotic lethal. In the F_2 the ratio obtained was 9 red : 3 purple : 3 eyeless (instead of 4 eyeless).

Combinations of either purple or eyeless in homozygous and the other in heterozygous condition are shown to be non-lethal.

54

COUSIN, GERMAINE. ***Analyse biométrique d'une hybridation interspécifique chez les Gryllides***

Au cours des 6 dernières années, j'ai entrepris un travail de génétique relatif à l'hybridation interspécifique de deux espèces de Gryllides: *Gryllus campestris* (*C*) et *Gr. bimaculatus* (*B*). J'ai obtenu les deux combinaisons de croisement: *CB* et *BC*. Ces hybrides F_1 se croisent entre eux et leurs parents sans restriction de fécondité. Tous les croisements avec ces hybrides donnent 12 combinaisons possibles. J'ai obtenu ainsi plus de 10,000 Grillons de toutes catégories, ce qui constitue un matériel unique pour une étude d'hybridation entre espèces. Dans la génération F_1, les Grillons *CB* et *BC* ont un caractère dominant provenant du parent (*B*)—les ailes caudées; et un caractère dominant provenant du parent (*C*)—la pubescence dorée sur tout le corps. De plus, les femelles *CB* et *BC*, ainsi que les mâles *BC* sont intermédiaires, seuls les mâles *CB* sont apparentés au Grillon (*C*) par la forme de la tête, ce qui semble ainsi être un caractère lié au sexe.

En raison de la position diversement intermédiaire des populations bâtardes selon le sens du croisement, l'analyse morphologique, même pour la génération F_1 fut impossible par les moyens ordinaires d'observation. J'ai donc du entreprendre l'analyse de cette hybridation par le méthode statistique et biométrique. Ces méthodes, si couramment employées en anthropométrie, m'ont amenée à préciser la notion et la valeur de l'indice morphométrique chez les Arthropodes.

Les mesures individuelles des termes d'un indice morphométrique approprié, mises en tableau de corrélation permettent, non seulement de séparer les espèces et les deux catégories d'hybrides *CB* et *BC*, mais encore de juger du degré de parenté des hybrides entre eux et leurs parents. En dehors de cet intérêt taxonomique, cette méthode de travail permet d'évaluer les caractéristiques générales des groupes, sans laisser ignorer les variations individuelles exceptionnelles, fait qui a une réelle importance lorsqu'on fait l'analyse d'un croisement. Ces tableaux de corrélation mettent également en relief l'intérêt spécial des indices allométriques, avec les données calculées qui les accompagnent, ils permettent alors d'apprécier toutes les caractéristiques comparatives des catégories de Grillons: hétérosis, dispersion, corrélation, allométrie et variabilité. Cette variabilité apparaît alors avec sa vraie amplitude et son vrai coefficient, non déformés par les calculs usuels autour de la valeur moyenne de l'indice. L'ensemble de ces données permet alors de dégager certaines lois générales de répartition des caractères parentaux aux hybrides.

Pour préciser la notion de l'espèce, comme pour analyser l'hérédité interspécifique d'animaux morphologiquement différents, on ne peut donc trouver de meilleure méthode de travail que la méthode biométrique ainsi comprise. Cette dernière peut s'imposer pour l'étude de tous les problèmes morphologiques délicats, non seulement ceux qui concernent la génétique, mais encore ceux qui concernent le polymorphisme à l'intérieur d'une même espèce.

55

CRAMER, W. ***Permanent Retardation of the Growth Rate of a Transplantable Mouse Carcinoma induced by Radiation***

If the cells of a rapidly growing transplantable mouse carcinoma strain are irradiated with sublethal doses of radiation and transplanted immediately afterwards, the resultant tumour A/1 shows a diminution in the growth rate, from which it rapidly recovers so that the growth rate of the original tumour strain is re-established. If, however, the tumour A/1 is again irradiated 8 days after the first transplantation the effect on the growth rate is intensified, that is to say, the effect of irradiation has become cumulative. By repeating this process a number of times and by using very small doses of radium rays it is possible to intensify this cumulative effect, so that eventually the growth of the tumour becomes stationary over a period of several weeks: the cancer cells have become dormant. If no further irradiation is applied when

this dormant state has been reached, the cancer cells recover gradually from the effect of irradiation; their growth rate becomes accelerated and they re-establish eventually the rapid growth rate of the original tumour strain. While this complete recovery has been observed in a number of experiments, an exception was found in one experiment in which the recovery was incomplete. The rapid growth rate of the original tumour strain was not re-established, but a new substrain established itself which grows at a much slower rate. This substrain has now maintained its slow growth rate over a period of 5 years. Irradiation has, therefore, induced a permanent biological change in the malignant cells of this tumour.

56

CRAMER, W. and HORNING, E.S. ***On the Association in Inbred Strains of Mice between the Brown Degeneration of the Adrenals and the Incidence of Mammary Cancer***

We have described a characteristic process of degeneration in the adrenals of mice—the brown degeneration—which can be induced in mice of mixed strain by the prolonged administration of oestrogenic hormones, but which develops spontaneously in mice of an inbred strain with a high incidence of mammary cancer. In this strain—the R III strain of Dobrovolskaia-Zavadskaia—the degeneration is very fully developed in both males and females at the age of 10 months, but it can be seen in its early stages already at the sixth month. The same process of brown degeneration has now been found in all the males and females of another strain with a high incidence of mammary cancer—the dilute brown strain—from the tenth month onward. In several other strains with a lower incidence of mammary cancer the brown degeneration develops at a later age, and then not as regularly and not as extensively. A further difference is that in the two high cancer strains (R III and dilute brown) the brown degeneration affects mainly the medulla, while in the low cancer strains its development is confined mainly to the zona reticularis of the cortex.

57

CRANE, M.B. and THOMAS, P.T. ***Reproductive Versatility in*** **Rubus**

A. THE MORPHOLOGICAL AND GENETICAL ASPECTS

The diploid species of *Rubus* investigated always reproduce sexually, whilst in polyploid forms and species reproduction may be (1) entirely sexual, (2) entirely non-sexual, or (3) partly sexual and partly non-sexual apomictic.

It has been found that *Rubus* species vary widely in the degree to which apomixis is developed. Not only do species differ, but a particular species will show a variation in behaviour depending on the species used as male in the cross-pollination.

Segregation has been found to occur within the non-sexual offspring and has given rise to new and distinctive types which in some cases breed true. This means that there are intermediate methods of reproduction, which, although superficially vegetative, have some of the properties of sexual reproduction.

B. THE CYTOLOGICAL AND EMBRYOLOGICAL ASPECTS

Cytological study has shown that parthenogenesis and apomixis are of frequent occurrence in Rubi. Segregation among non-sexual offspring indicates that the apomictic embryo develops at some stage subsequent to the first division of meiosis, and evidence has been obtained that fusion of nuclei within a haploid embryo sac can occur.

New forms commonly arise through hybridization and chromosome duplication, and cytological evidence shows how far these factors associated with apomixis are involved in producing new species in nature and new cultivated forms such as Veitchberry and loganberry (*R. Loganobaccus*). Such common occurrence of chromosome duplication by the formation of unreduced gametes is probably symptomatic of apomictic behaviour in *Rubus*.

58

CREPIN, C., BUSTARRET, J. et CHEVALIER, R. ***Création pour la France de blés résistants à la Carie***

Les variétés de Blé cultivées en France sont toutes sensibles à la Carie (*Tilletia Tritici* (Bjerkander) Winter; *T. caries* Tulasne). Aucune des variétés résistantes actuellement connues ne convient aux conditions climatiques et culturales de la France. D'où les recherches que nous poursuivons depuis 1927 pour créer des variétés résistantes et utilisables chez nous.

Nous avons déterminé la réaction d'un grand nombre de variétés vis-à-vis de plusieurs provenances de Carie, étrangères ou françaises, lesquelles ont montré des propriétés pathogènes très différentes. Ceci confirme l'existence de "formes physiologiques" de Carie, mises en évidence par de nombreux auteurs.

Les provenances françaises essayées ou bien infectent ou bien respectent les variétés *Baulmes*, suisse, et *Magyarovar*, hongroise; par contre, elles n'infectent ni *Hussar* ni *Martin*, donc seraient classées par les auteurs américains parmi les "formes" les moins virulentes (formes T_1, T_2 et T_3 de Rodenhiser et Holton).

Les notions de "provenance" et de "forme" de Carie n'ont rien de comparable à la notion de "variété pure". Une provenance de carie est assimilable à une population; composée de types morphologiquement et physiologiquement différents. Pour faire son analyse, c'est-à-dire déterminer les formes physiologiques qu'elle renferme, plusieurs méthodes existent:

(1) isoler des lignées monosporidiales, les apparier deux à deux, et infecter des hôtes différentiels convenablement choisis (Flor, Hanna, Mlle Becker);

(2) multiplier la provenance considérée sur plusieurs variétés-hôtes douées d'un certain degré de résistance: nous avons pu ainsi isoler, dans plusieurs provenances, des formes très virulentes à l'égard d'une ou plusieurs variétés;

(3) utiliser séparément comme matériel infectieux le produit d'épis cariés battus un à un.

La première méthode est bien la plus précise et la plus sûre. La dernière, imaginée par nous et essayée en 1937 et 1938, a donné d'excellents résultats; elle permet un inventaire facile des formes qui existent dans une région donnée.

Malgré la difficulté de l'analyse génétique précise du caractère "résistance à la Carie", un grand nombre de croisements, entre variété sensible et variété résistante ou entre deux variétés résistantes à une forme donnée de Carie, ont conduit aux constatations suivantes, valables dans tous les cas étudiés par nous:

(1) La résistance à la Carie est un caractère mendélien; aucune corrélation n'apparaît entre cette résistance et un autre caractère.

(2) Le caractère "résistance" est commandé par plus d'un facteur. Il paraît souvent bifactoriel, par exemple chez *Martin* et certains de ses descendants hybrides.

(3) La résistance à une forme donnée de Carie peut, chez des variétés différentes, être commandée par des facteurs différents. Inversement, chez une variété donnée, la résistance à plusieurs formes peut être commandée, soit par les mêmes facteurs, soit par des facteurs différents. Assez souvent apparaissent, dans la descendance d'un croisement, des types transgressifs, plus résistants ou plus sensibles que chacun des deux parents.

La résistance à la Carie étant un caractère indépendant peut, sur un type hybride, être associée à tous autres caractères désirables empruntés à un géniteur sensible. Par croisement entre variété américaine ou allemande résistante et variété française sensible, nous avons obtenu des types résistants et tout près de convenir aux conditions climatiques et culturales de la France: plusieurs ont été recroisés soit avec des blés français, soit avec des blés résistants à d'autres formes de Carie. Dans un avenir assez proche, nous pourrons mettre en multiplication des variétés nouvelles aussi productives que les variétés françaises actuellement cultivées et douées d'une bonne résistance à la plupart des formes de Carie connues.

Ces travaux entrent dans le cadre général de nos recherches pour l'obtention de variétés nouvelles résistantes aux principaux accidents et maladies qui menacent le blé dans notre pays: gelées de l'hiver, rouille jaune, rouille noire, charbon, etc.... Sans qu'il soit nécessaire de mener jusqu'au bout, pour chacun des caractères recherchés, une analyse génétique complète, la connaissance des lois générales de l'hérédité permet de mettre au point les méthodes qui conduisent, plus ou moins rapidement, mais sûrement, à la solution de ces problèmes respectifs.

Nota. L'exposé de nos travaux et une mise au point de l'ensemble des données que l'on possède sur la question, avec bibliographie complète ont été faits par nous dans:

(1) "Le problème de la création de blés résistants à la Carie." *Ann. Epiphyt.* 3, 323–439.

(2) "Nouvelles recherches sur la résistance des blés aux caries." *Ann. Epiphyt.* 4, 413–47.

59

CROWFOOT, DOROTHY. ***Recent Work on the Properties of Crystalline Proteins and Viruses***

Proteins as crystals may be said to have a very close connexion with the living cell, since protein crystals were first observed occurring naturally in plant cells. In studying protein molecules as they exist in crystals (particularly in wet crystals) we are studying them therefore under conditions essentially similar to those obtaining in living tissues.

As a class the proteins which crystallize readily all belong to the group which have been named corpuscular proteins. In the ultra-centrifuge they behave as roughly globular bodies of high but definite molecular weights, and X-ray measurements on some seven different proteins provide general confirmation for these findings. The X-ray photographs further illustrate the great effect of the medium on the behaviour of proteins. Crystals photographed wet in their mother liquor show X-ray reflexions extending to spacings of 2A. corresponding to regularities in the structure down to atomic dimensions. On removal from the liquid most protein crystals, e.g. lactoglobulin and haemoglobin, shrink, often visibly, and the new crystal structures formed are disordered, giving very few X-ray reflexions. In the wet crystals of these proteins the molecules are held apart by considerable sheaths of water, and variations in density that have been observed as the immersion medium is changed suggest that in some cases their equilibrium distance apart may also vary. Remarkable changes of this sort have been observed with tobacco mosaic

virus proteins in solution, where the equilibrium distance varies from 320A. at *p*H 7 to 175A. at the isoelectric point (*p*H 3·4). It is possible to explain this behaviour in terms of the theories recently developed by Langmuir and by Levine. The long-range forces of attraction are due to the ionic atmospheres surrounding the virus particles and necessarily vary with *p*H and salt concentration.

In most protein crystals it is impossible from the present X-ray data to draw direct conclusions as to the existence of actual molecules, let alone the distances between them or their exact internal structure. Insulin has, however, a particularly simple crystal structure, and here the analysis may be carried a stage further. It is possible to calculate both for wet and dry insulin vector diagrams which show prominent interatomic distances within the structure. The main pattern around the origin in both cases corresponds to strong interatomic distances of approximately 10 and 20A., the pattern being shifted through a small angle in passing from the wet (expanded) to the dry (collapsed) crystal structure. The shift both provides evidence that there is a molecule present and demonstrates the interatomic distances that occur to a first approximation within any one molecule. The relations observed suggest that the insulin molecule is built of subunits roughly 10A. across packed in some variety of cubic close packing.

These 10A. distances relate the crystal structure of insulin on the one hand with the fibre proteins, and on the other, still more closely, with the virus proteins. The structure of the tobacco mosaic virus particle as determined by J. D. Bernal and I. Fankuchen is peculiarly interesting. The virus particle itself behaves as a single crystal with a hexagonal unit cell $a=87$ A., $c=68$ A. The particle diameter 152A. corresponds to the aggregation of only three of these units while the length is probably at least 22-24 times the length of the crystal unit in this direction. Within the unit cell there is evidence of further subdivision, first into a pseudo-rhombohedral unit one-sixth in size, then into flat platelets $44\times44\times22$A. arranged in a cubic close-packed array, and finally into subunits $11\times11\times11$ A.

The structure of these crystallographic subunits is still highly speculative and calls for further investigation.

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Csik, L. *Sauerstoffverbrauch der* **Drosophila-***Puppen verschiedenen Genotypus*

Die Mutationen *miniature* (*m*), *dumpy* (*dp*), *cut*^{6} (*ct*^{6}) und deren Kombinationen wurden auf den O_2-Verbrauch der Puppen hin untersucht.

Methode. Puppen bekannten Alters wurden unter gleichartigen Bedingungen bei 24·5° C. aufgezogen; kurz vor dem Schlupfen wurde ihr Sauerstoffverbrauch mit dem Warburgschen Apparat bestimmt. Die Unterschiede im Sauerstoffverbrauch wurden sowohl pro Puppe wie pro mg Trockengewicht berechnet.

Ergebnisse. Alle Mutanten zeigen im Vergleich mit den Wildtyp eine statistisch gesicherte Verringerung des O_2-Verbrauchs. Unterschiede wurden auch zwischen einzelnen der Mutanten und Mutanten-Kombinationen festgestellt. Ein Vergleich zwischen der Wirkung der Gene fur sich und in Kombination (*m dp*; *m ct*^{6}) ergab dass die Wirkungen sich weder addieren noch einen Mittelzustand herbeizufuhren, sondern dass diejenige Mutation, die den Sauerstoffverbrauch des Wildtyps starker herabsetzt, ausschlaggebend ist für den Sauerstoffverbrauch der Kombination, in welcher sie enthalten ist.

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Csukás, Z. *The Genetics of the Lactation Curve*

The shape of the lactation curve is defined by the degree of declination in milk production during 10 weeks after calving, of those cows conceiving in that time. Differences in the shape of the curve have been observed in the same individual in successive lactations, even under the same environmental conditions and at the same season of calving. At least three lactations are necessary for determining the characteristic shape of the curve for any cow. The shape of the curve is hereditary, homomeric genes being involved.

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Curtis, Maynie R. and Dunning, Wilhelmina F. *Host Constitution and the Incidence of Chemically-induced Tumours*

Observations were made on the occurrence of 2751 malignant tumours at sites of injection into the subcutaneous tissues of rats of 3, 4-benzpyrene in paraffin wax. Rats of several inbred strains of ages varying from 30 days to 2 years were injected. The quantity of benzpyrene was varied from 0·2 to 24 mg. per rat. Three concentrations of the chemical (1·0, 0·25 and 0·1 %) were used. The surface area of the tissue exposed to a given quantity of the 1·0 % concentration of the carcinogenic chemical was varied by injecting the mass in discrete nodules of 0·2, 0·1 or 0·05 c.c. volume.

Variation in concentration of the carcinogenic chemical was more effective in influencing the prob-

ability of the malignant change and the average time of its occurrence than was variation in surface area of tissue exposed to the chemical or host constitution.

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DAHLBERG, G. ***A Method of Deciding Dominance or Recessivity of Polymoric Inheritance***

The author shortly reviews his system of dividing up characters from the point of view of heredity (cf. Gunnar Dahlberg, *Die Vererbung der Allergischen Disposition*, *Fortschritte der Allergielehre*, Basel, 1939). From a practical point of view the characters may be classified into three groups:

(1) *Purely hereditary characters*, i.e. characters with no appreciable or only a very small range of variation caused by environmental factors (for instance, colour blindness).

(2) *Characters determined by environment.* The genes necessary for such characters must be present in practically all human beings (for instance, typhus).

(3) "*Constellational*" *characters* which require a meeting of environmental and hereditary factors (for instance, poliomyelitis).

The question of dominance and recessivity by complicated modes of inheritance is discussed. If a character is quantitative it usually has a certain range of variation which may be due to environment or to genes. By deciding the variation among the offspring of parents who are both extreme variants, indications of the underlying mechanism may be obtained. As an example we may take stature. If the parents are extremely tall individuals the offspring will show less variation than in the population as a whole. By comparing the variation of the offspring of a group, where both the parents are extremely tall, with a group where both the parents are very short, the result will differ if it is mainly a question of dominance or of recessivity. If small stature is due to dominance there will be a larger variation among the offspring of the short parents than among the offspring of tall parents. Of course due regard has to be paid to the relation between the variation and the mean (e.g. by using the coefficient of variation). Offspring of parents who are cousins may be analysed in a similar manner.

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DAHLBERG, G. ***Rare Psychological Defects from the Point of View of the Population***

When discussing man's heredity we may view the problem from two angles. One is to look at it from the viewpoint of the individual, asking: What hereditary composition will characterize the descendants of a given person about whom we have certain information? We know something about his personal characters, and we know something about the characters of his relatives, etc. On the basis of our knowledge about how characters are inherited, we are in some measure able to make a prognosis. Conversely, an investigation may aim at elucidating a hereditary mechanism in order to make a more definite forecast possible. We may also look at the problems from the point of view of the population, asking whether it is probable that the hereditary make-up will keep constant in the population or become modified in one or the other direction under given conditions.

It is only in recent years that the human problems of heredity have been viewed from this angle. One may perhaps venture to remark that there existed till recently an English school working along statistical-mathematical lines without building on the foundation of Mendel's discoveries. There also existed a continental school trying to show that Mendel's laws apply to man, and to find out what hereditary factors, or hereditary mechanisms, determine different characters without always paying due regard to the special statistical requirements of such analysis. A synthesis of these schools has only recently developed. To-day we see the beginning of a scientific movement which, by employing statistical-mathematical methods, tries to investigate the relevance of Mendelism to man, and particularly to human populations in their entirety.

In trying to do this, one has to find a point of departure for argument. It is generally assumed that marriages are contracted at random and that fertility is also determined by a random mechanism. A mechanism of this type is called amphimixis.

Now it might be maintained that we are often justified in reckoning with amphimixis. It is also obvious, however, that deviations which may be of importance, occur as well. So far as I can see, the latter may be classified under five headings, namely, selection, inbreeding, assortative mating, isolate effects, and mutations. Thus, if a person does not marry at random, he or she may act as follows:

(1) Fail to marry, or have fewer than the average number of children—a mode of behaviour which corresponds to *selection.*

(2) Marry a relative to a greater extent than what is demanded by chance (*inbreeding*).

(3) Choose a person with a given character (*assortative mating*).

(4) Restrict choice of a partner to a limited circle (*isolate effect*).

(5) Produce gametes of a new type (*mutation*).

So far as I can see, there are no further theoretical possibilities of any importance. The point is conse-

quently to find out in what way the hereditary make-up of a population is modified by processes of the kinds already specified. Of these there are two that produce actual changes in hereditary make-up, viz. selection and mutation. By mutations new genes arise. By selection the frequency of the genes may be modified and genes may disappear. Assortative mating and in-breeding, like isolate effects, only bring about a grouping of genes other than the one if amphimixis occurred. All three result in an increase of homozygosity and a decrease of heterozygosity, as compared with what would happen in an ideal system of random mating.

When investigating the presence of rare defects of a more serious nature, for instance the incidence of mental deficiency, we should in the first place ask whether processes of the type suggested above affect the frequency of characters. To begin with, we might ask what part is played by mutations. It seems most plausible to assume that genes determining serious defects have arisen by mutation. It is, however, improbable that mutation frequency is so high that the frequency of characters will be affected from generation to generation during a moderately prolonged period.

The question then arises: Is selection capable of affecting the gene frequency? The result of selection is that very serious defects, due to single dominant genes which manifest their effects at an early age, never spread at all. Individuals with the grave defects under discussion hardly ever propagate. Consequently in practice most defects which spread through inheritance must be recessive, or dominant *dihybrids*, or be inherited in a still more complicated manner. If the propagation of defective individuals is small, we should expect some effect of selection and a decrease in their frequency. However, this effect is very small in the case of rare hereditary characters, as particularly shown by J. B. S. Haldane. Selection can only begin to have an effect when the heterozygotes have attained a certain frequency. I have termed this limit the "lowest heterozygote frequency". We can never force a gene below this limit. A practical example of the ineffectiveness of selection in such limiting cases is afforded by the *amaurotic idiocy*. Individuals suffering from this form of idiocy die at about the age of sex-maturity and never propagate. In spite of this, four to five such idiots are annually born in Sweden, and there are almost 100 in our population.

In such circumstances sterilization must be ineffective in regard to the frequency of rare defects, even though from an individual point of view it may be justified. The majority of grave defects ought to keep in the neighbourhood of the lowest heterozygote frequency. As individuals of this type have been leading a life on the verge of destitution for thousands of years past and have had hardly any opportunities worth speaking of for propagation, they have consequently been subjected to a selection which has forced them down to the frequency minimum. Doubtless, therefore, it will be impossible to gain anything by sterilization. We might say that the fact that sterilization, etc., has no effect on rare, recessive characters, is also advantageous. If those rare forms of intelligence which mean a capacity for independent thinking, are inherited recessively, it will be impossible by persecutions or other measures aimed at intelligent persons, to exterminate individuals of this type in a population.

So far as assortative mating is concerned we may assert in regard to rare defects that such a process cannot be important. The fact that a defect is rare, excludes the possibility that those who have the character will meet.

The question then arises: Might we not be able to lessen the frequency of rare defects by prohibiting cousin marriages? If one could prevent a large number of cousin marriages in cases of very rare genes, a very considerable effect would be obtainable. However, a population is composed of isolates. In a large isolate, a gene may be rare, but if so we should not expect a considerable number of cousin marriages. Conversely, it is true that comparatively many cousin marriages may take place in a *small* isolate, but then the gene cannot be so very rare. Consequently, we cannot expect to find simultaneously in a population both rare genes and numerous cousin marriages. In point of fact, the frequency of genes and the incidence of cousin marriages are balanced in such a way that it would be possible to lessen the incidence of a character by 15 % of the character frequency. The postulate for obtaining such a figure is that the gene lies at the limit of the lowest heterozygote frequency, and that the character is inherited as a simple recessive character. In more complicated forms of inheritance the effect becomes smaller. A prohibition of cousin marriages would in any case have a much greater effect than sterilization, but yet have a comparatively moderate one.

It now remains to discuss rare defects from the point of view of isolates. The term "isolate" was first defined by Wahlund and myself; by an isolate we mean a geographically delimited group, a village, etc., within which we are fairly justified in assuming random mating. We also speak of social isolates in so far as people marry within a given social stratum. Actually, the isolate boundaries are not distinct, a fact which should be borne in mind in calculations carried out on isolates.

Since a population is made up of numerous isolates we might assert that, as a rule, we may find the genes of a given very rare defect in a given isolate but

probably not in an adjacent isolate. Crossings beyond the isolate boundaries therefore are less dangerous than crossings within the isolate boundaries. It is further evident that a mutation in a large isolate has smaller chances of leading to homozygosity than a mutation in a small isolate. From the point of view of defective mutations the small isolates are therefore more dangerous than the large isolates.

To human populations the fact that isolate boundaries are now in process of breaking up is highly significant. The incidence of cousin marriages is, as implied above, a measure of the size of isolates. Now the frequency of cousin marriages has decreased considerably towards the present time. In 50 years, for instance, that is to say from 1876–80 up to 1926–33, the frequency of cousin marriages in Bavaria decreased from 0·87 to 0·20 %. In part, this was due to the fact that the isolates increased in size. When a population grows in number, the separate isolates will also increase, and an increase of this type is without significance to the frequency of defectives.

However, there is no doubt that the decreased frequency of cousin marriages is to a significant extent due to breaking up of isolates through the growth of communications and through migration into the towns. This breaking up of isolates may be said to imply that the isolates ought on an average to be doubled and perhaps even trebled. This must have lessened considerably the frequency of defective homozygotes. If the isolates are doubled in size, the number of defectives must have decreased by half. The increase in the number of idiots and other defectives which has occurred in most countries according to their official statistics, under such circumstances must be due to an improved registration. In Sweden population statistics are comparatively reliable, but nevertheless a special investigation has shown that only about 50 % of the idiots are registered in the official statistics. In other words, statistical data are so unreliable that in spite of an actual decrease of defectives we may expect for a long time to get an apparent increase.

Before finishing I want to point out that defectives apparently play no decisive part in a population. Though a population may have a higher or lower percentage of defective individuals the difference may have very little significance, even if one wanted to help these unfortunate individuals by effective financial assistance. A question of greater importance is: How do processes of the nature suggested above affect ordinary characters, particularly the standard of intelligence and the social effectiveness of a people? As I have mentioned before, this process results in an increased heterozygosity. If genes which determine social effectiveness are chiefly dominant ones, the breaking up of isolates must be an advantageous process. If desirable genes are recessive the process must have a noxious influence, and if dominance and recessivity are balanced the process may have no noteworthy effect.

In order to illustrate one of these possibilities I shall discuss another character, namely, stature. In Sweden stature has increased by 9 cm. in 100 years. In part this increase may be due to an improved standard of living. There is, however, some reason to believe that the breaking up of isolates also plays a part. Pairs of genes determining tall stature have been present in different isolates, and in a more or less homozygous form. By the breaking up of isolates the genes have become disseminated in the population and this has resulted in an increase of stature. A process of this type may occur during many generations before an equilibrium is gradually reached. If the same applies to genes determining intelligence and social effectiveness a breaking up of isolates will result in a decrease in the number of exceptionally stupid people, an increase in the average intelligence and an increase in the number of geniuses. But it may also happen that this process acts in an opposite direction, bringing about a decrease in the average intelligence and an increase of stupid people. Indeed, it may be that the same processes do not occur in different populations. At present we cannot make any definite statements about the significance of this process. In such circumstances, investigations into the more detailed mechanism of the behaviour of genes determining social effectiveness, intelligence, etc., are of very great interest.

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DANTCHAKOFF, VERA. ***The Genetic Determinants of Sex in Higher Vertebrates***

Chemical substances, as represented by the sexual hormones, exert characteristic effects in the normal organism; in the adult a number of tissues are stimulated by them, while in the juvenile animal a precocious realization of certain developmental processes may be achieved. Replacement therapy with the sex hormones indicates the importance of these substances in maintaining sex characters in castrated animals showing regressive changes in these tissues following the removal of the gonads, but such experimentation is of little value in determining the causes of initial sex differentiation. In regard to this point it may be argued that if the products of the secretory activity of the gonads determine processes of differentiation which are only stimulated following the differentiation of the sex glands such activity could not precede the organization of these. It may be true that the differentiation of an ovary cannot be

determined by a chemical substance which will later be produced by it, but, since the cells of the gonad anlage possess a special constitution, a chemical substance of the same nature may be produced from a special type of metabolic activity in these undifferentiated cells.

It has been shown by experiment that the introduction of the sex hormone into an organism before the processes of sexual differentiation on the gonads are completed can affect not only the differential proliferation of tissues of the gonad anlage of the opposite sex to that from which the hormone has been derived, but also the differentiation of the accessory sexual organs and other somatic characters. It is established that the primary manifestations related to genetically determined sex may be overridden by this method.

If the processes leading to the development of normal, genetically determined sexuality are compared with those obtained experimentally two differences are found. First, it is not possible by experimental means to exclude completely those characteristics relating to the genetically predetermined sex and, secondly, the administration of hormone cannot be done either early enough, or in a properly balanced manner to simulate the natural reaction between hormone and gonad anlage in the organism.

In spite of this the results of experiment and nature are similar in many respects, although the sex changes induced may exhibit only a temporary phase. It is found also that the introduction of the hormone disproportionately stimulates some of the heterologous processes while others again are not inhibited sufficiently.

These differences do not allow of the argument that the primary substances involved in natural sex differentiation are fundamentally different from the substances used experimentally. The similarity in the histogenetic processes evolved spontaneously and those induced by hormone is a function of the similarity of the embryonic tissues in both sexes and of the mechanism acting upon them. The differences which appear are conditioned by the presence of a double-acting mechanism in one case and a single-acting one in the other. The chemical factor is an agency in genetic determination of sex differentiation; it initiates the process even if it does not completely control the subsequent differentiation.

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DARLINGTON, C.D. *The Prime Variables of Meiosis*

The first act by which we distinguish meiosis from mitosis is the pairing of the chromosomes to give the double pachytene threads. This process conditions all the later special properties of meiosis such as crossing-over and chiasma formation, co-orientation of the centromeres and reduction of the chromosome number. It is therefore of the first importance to know the conditions limiting and varying its occurrence.

The most obvious of such variables is the *time limit*. In many plants and animals with large chromosomes pairing is interrupted before it is complete, so that crossing-over and chiasma formation are necessarily localized in the region where pairing began, in *Fritillaria*, for example, near the centromere. In *Chrysochraon*, *Mecostethus* and elsewhere we find localization in two regions, centric and distal. And finally in tetraploid species of *Tradescantia*, the chiasmata are entirely localized near the ends of the chromosomes, and it is probable that here we have a purely terminal localization of pairing. It seems that pairing begins either at the ends of the chromosomes or at the centromeres.

Now if localization is in fact due to the operation of a time limit we should expect that it would be increased by any reduction in the rate of pairing such as would arise in (i) structural hybrids, including species crosses and haploids, (ii) gene asynaptics, (iii) tetraploids as compared with related diploids, (iv) female mother cells, as compared with male, in pure forms and hybrids.

A preliminary survey shows that localization is indeed increased where pairing is hindered or delayed. It may be terminal as in haploids, hybrids and asynaptics of *Triticum*, or centric as in hybrids and female mother cells of *Lilium*. And, further, the more the chiasma frequency (and consequently the metaphase pairing) is reduced, the more extreme is its localization. The case of the *Tradescantia virginiana* complex is instructive, for the tetraploid forms have in general a lower chiasma frequency and a higher localization than the diploids. Pairing is evidently delayed by the greater number of chromosomes. This suggests that the chiasma frequency might be used alone as an index of localization, where movement of chiasmata may conceal their original positions, and Upcott has accordingly found that there is a *reduction factor* of 0·84-0·97 for the chiasma frequency of tetraploids as compared with parental diploids. Again, this effect is greatest where the chromosomes are largest.

This application of the precocity theory therefore provides a simple explanation of a number of properties of chiasma frequency and distribution in hybrids, mutants and polyploids, and it is probably a sufficient explanation of many of them.

The all-or-nothing effect of chromosome pairing, however, is only the first variable affecting crossing-over and chiasma formation. Parts of chromosomes

and even whole chromosomes, particularly in asynaptics, may pair at pachytene and later fall apart without crossing-over. In such cases we may suppose that the torsion of relational coiling has failed to reach the threshold for crossing-over. Unpaired parts of chromosomes can develop coiling, so we may suppose that chromosomes can pair when their internal torsion is partly undone. Similarly, the combined statistical and individual observations of chiasma frequency and distribution that Mather has brought together in discussing *competition* and *position determination* indicate (what is indeed *a priori* probable) that the torsion developed in the paired chromosomes is not uniform throughout their length. It has a characteristic relationship with the centromere, or perhaps with the place where pairing began, and also characteristic properties for the nucleus as a whole. Where to draw the line between non-pairing and reduced coiling we do not yet know, but all these properties indicate that chromosomes are undoing their coiling while they are pairing.

By such arguments we can recognize the prime variables of meiosis as time limit and no time limit, centric and terminal localization, high and low torsion, and so on. The astonishing property we then discover is that all species, and even first crosses of species so far studied, have a uniform behaviour for the whole complement of the individual. Maeda's derivatives of *Allium Cepa* × *fistulosum* prove the importance of this rule, for not only do they recombine all the prime variables in different individuals but they show the breakdown of this law of co-ordination within individuals. Analysis of this kind can be used to test the mechanical and genetical principles underlying both the control of meiosis and the character of the species.

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DAVIDSON, H.R. ***Practical Aspects of Improving Pigs***

Modern methods of improving pigs by breeding are based largely on testing and recording. Under these methods stock are selected, or are supposed to be selected, on their own records of production or on the records of production of their progeny. The assumption is that merely by mating together stock with good production records the average level of efficiency for the country, in those characters in which heredity plays the principal part as contrasted with nutrition or other environmental factors, will be raised. It is submitted that this assumption is not justified. Nutritional and environmental factors operating before weaning play a more important part than has so far been generally accepted. Selection on records of production has in practice encouraged the attainment of "record" production, i.e. a maximum level of production instead of an optimum level. This has the objection from the point of view of the individual that maximum levels may not be as profitable as lower ones, and from the point of view of the industry as a whole that the attempt to raise the average level of production of the whole by considerably increasing the level of some individuals decreases instead of increases the general degree of standardization.

The number of pedigree boars which have been selected on a basis of performance is very small indeed in relation to the number of commercial sows kept for breeding. Existing methods of testing and recording are therefore unlikely to produce any important improvement in the general level of profitability or of standardization until some control over breeding is exercised. On the other hand, owing to financial difficulties associated with commercial competition, with different environmental conditions and with varying prices of feeding stuffs, much of the testing and recording carried out at present is genetically unsound.

For these reasons it is submitted that the application of technical methods of improvement, such as testing and recording, will not lead to a satisfactory amount of improvement until a scheme of boar licensing is inaugurated, and that until the technique of breeding according to performance records, and the different effects of breeding and nutrition are more fully understood, the testing and recording of pigs should be restricted to a small number of herds under careful research supervision.

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DAY, BESSE B. and AUSTIN, L. ***The Use of the Three-dimensional Quasi-factorial Design for Testing a Large Number of Ponderosa Pine Progenies***

An important phase of forest genetics work at the California Forest and Range Experiment Station, U.S. Forest Service, is the selection of seed trees for breeding and mass reforestation. For this purpose it was deemed necessary to examine a large number of individual seed trees, comparing them by means of their progenies. Such an experiment of 729 seed selections (696 Ponderosa Pine and 33 Jeffrey Pine) was sowed at Placerville, California, in the early spring of 1937.

To minimize the effect of the heterogeneity in growing conditions arising from so large a seed bed smaller blocks were required than would have been

needed for a complete replication, the ordinary randomized block design. The design adopted was the three-dimensional quasi-factorial with three groups of sets (Yates, 1936) where $9^3 = 729$, the number of progenies, formed a perfect cube with nine plots to a block and 81 blocks to a replication. The requirements of this design are that the plots of a replication be grouped in three different ways, each individual progeny appearing not more than once in the same block with any other, and that the blocks of each group cut across those of the other groups. The groups, *X*, *Y*, and *Z*, were each replicated three times, making a total of nine replications, 6561 plots in 729 blocks.

This paper reports on the effectiveness of the design for eliminating variations in the two principal measurements, two-year height and diameter, due to unavoidable differences in treatment and seedbed environment. The procedures for adjusting the original progeny height and diameter measurements are accordingly applied.

Two methods for doing this are available, yielding the same intra-block error term. In the first (Yates, 1936), inter-block effects are ignored, and the error term for testing differences of progeny means is based entirely on the intra-block error. The second method (Yates, 1939), somewhat more precise, makes use of the information from the inter-block comparisons as well as that from the intra-block comparisons. The nature of this design, more blocks than replications, results in a partial confounding of blocks with progenies. Hence, in the procedure for recovering inter-block comparisons, the analysis follows that of a factorial experiment of three factors, *U*, *V*, and *W*, each of three levels. In the *X* replications the main effects *V* and *W* and interaction *VW* are confounded with blocks; in the *Y* replications *U*, *W*, and *UW* and in the *Z* replications *U*, *V*, and *UV*. Two types of comparisons are available for each of these, one from inter-block differences and the other from intra-block. The relative weight of each of these is estimated from the measurements themselves, and hence should be quite precise because of the large number of degrees of freedom on which they are based. Inter-block mean square error is based on 504 degrees of freedom, for which the sum of squares are entirely free of progeny effects; the intra-block means square error on 5104 degrees of freedom.

The inter-block mean square of the diameter measurements was 1073, the intra-block 198·77. The ratio of relative weights is 5·4. The ratio of the efficiency of this design, with the inter-block information recovered, to the ordinary randomized block is 130 %. This is sufficiently large to indicate that the three-dimensional lattice was definitely superior for this experiment. Also 5 % efficiency is gained by recovering the inter-block information rather than ignoring it as in the original procedure.

The variances for comparing progenies are 48·07, 50·14 and 50·39 depending on the relative block location of those being compared. The mean variance of all comparisons is 50·25. The mean of all plots, each of which is the sum of six seedlings, is 147·7, the measurements being taken in 0·01 in.

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DEMEREC, M. *The Nature of Changes in the White-Notch Region of the X-chromosome of* Drosophila melanogaster

One of the most interesting questions which genetics has not been able to answer is: What is the mechanism responsible for mutations? Although we are not ready to give the final answer, it is evident that this mechanism is a complicated system, sensitive to disturbances, and readily reactive to changes. With the recently developed cytogenetic technique a tremendous forward step has been made in showing some of the intricacies of that system. This technique has been used in the work which will be reported here, where an intensive cytogenetic study was made on more than one hundred X-ray induced changes in a short section of the *X*-chromosome. The results of this study give further evidence of the existence of a sensitive balance between genes and their genic environment, and indicate that identical mutant types may be caused by different changes and that similar changes may produce different mutant effects.

In this presentation the following mutants and their symbols will be used: prune (*pn* 0·8), white (*w* 1·5), roughest (*rst* 1·7), facet-Notch (*fa*, *N* 3·0 ±), diminutive (*dm* 4·6), echinus (*ec* 5·5) and bifid (*bi* 6·9). The number in the parenthesis indicates the position of the locus on the linkage map prepared by C. B. Bridges for DIS-9.

MATERIAL

All changes which will be discussed in this paper were found in the F_2 generation raised from matings between females which were untreated and males which had been X-rayed with about 2500–3000 r. units at about 0·72 A.

The material which will be described here has been accumulated from experiments conducted during the last seven years. The cytogenetic analysis of fourteen of these cases has been already published by Slizyńska (1938). Miss Margaret E. Hoover and Miss Eileen Sutton helped with the cytological analysis of the material, and Miss Eunice White helped with the breeding work. To them the author wishes to express his appreciation.

Observed types of changes

The induced changes observed in this region of the chromosome fall into several well defined groups and types. The frequency of the occurrence of each type is shown in Table 1.

Table 1. *The frequency of various induced changes in the white-Notch region*

		Chromosomes				
		Not aberrant		Aberrant		
		Deficient				Hetero-chromatin involved
	Total	No	Yes	No	Yes	
Stable changes:						
Viable, fully studied	11	11	—	—	—	—
Viable, not aberrant	17	—	—	—	—	—
Lethal changes	44	3	30	10	1	2
Unstable changes	30	—	—	29	1	30
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Stable viable types

This group includes the viable changes to white and its allels. The experimental set-up was such that the viable changes in the Notch locus could not be detected. The cytological analysis of twenty-eight cases indicates that none was connected with either a translocation or an inversion. Eleven of these cases were studied carefully, band by band, for small inversions, deficiencies and differences in band intensities. None has been observed. This group, therefore, represents changes not related to any cytologically detectable aberrations. It seems probable that these types represent gene mutations due to chemical changes in the gene molecule of the white locus.

Lethal types

The second group of changes consists of lethal types involving the white locus, the Notch locus, or both. The forty-four cases studied in this group fall into two classes. Among thirty-three cases with no aberrant chromosomes, that is, with no inversions or translocations, thirty cases showed deficiencies of from 1 to 50 lines, while three cases showed no cytologically detectable deficiency. On the other hand, among eleven cases showing chromosomal rearrangements only one deficiency was observed, the remaining ten cases having all lines present. Since this distribution is found in an unselected sample there can be little doubt as to the significance of the difference between the two classes. The data show clearly that the lethal changes in both the white and the Notch loci, when not associated with chromosomal rearrangements, are in a majority of cases cytologically detectable deficiencies. When, on the other hand, they are associated with chromosomal rearrangements, they are in a great majority of cases not deficiencies.

Before drawing any conclusion from this observation let us consider the question of the biological effects of these two cytologically distinguishable types of lethals. All Notches of this group are invariably lethal in homozygous and hemizygous condition. Their most characteristic phenotypic effect is the notching of the wings and the delta-like thickening of the wing veins. Comparative studies on a number of Notches indicate that although the Notch phenotype may be modified by various environmental and genetic factors, the intensity of notching is not correlated with the length of the deficient region. In other words, on the average, the phenotype of a Notch showing a fifty-line deficiency does not differ from the phenotype of a Notch showing no deficiency. It appears probable that the Notch effect is produced when a certain specific region of the chromosome represented by 3 C7 line is affected, and that the extension of the deficiency on either side of that region produces no effect on the Notch-phenotype. Ten Notches of this group, including both deficient and non-deficient types, were tested for the cell-lethal effect and all were found to be cell-lethal. All biological tests, therefore, suggest that, so far as the biological effect is concerned, there is no difference between the deficient and non-deficient Notches. There can be no doubt that in the case of long deficiencies the Notch effect is produced by the absence of the Notch locus, namely, by the elimination of the activity of the Notch locus from the gene complex. Since the biological and the phenotypic effect of both the deficient and non-deficient Notches is identical, it follows that either the non-deficient Notches are minute deficiencies indiscernible with the present technique, or that in these cases we are dealing with changes in the locus which either eliminate or suppress the activity of the gene. The evidence which is presented here seems to favour the second possibility. Thus, the Notch phenotype may be considered to be due to the suppression of the activity of the Notch gene, and may be caused either by the absence of the gene or by a change in its activity.

We can now return to the consideration of the difference in the distribution of deficient and non-deficient Notches among the two groups, one having chromosomal rearrangements and the other not. As has been mentioned before, about one-tenth of the Notches with normal chromosomes are not deficiencies, while in the aberrant group about nine-tenths are of that type. This suggests a relationship between the non-deficient Notches and the chromosomal rearrangements with the break adjacent to the Notch region. If the Notch results from the suppression of the activity of the gene, then this evidence

indicates that the incidence of such suppression is much higher when the locus is taken out of its normal sequence and attached to some other region of the chromosome. This is equivalent to saying that the suppression of the gene activity is brought about to a large extent by the change in the position of the gene. In these cases, therefore, the chemical constitution of the gene may not be affected at all, but the activity of the gene may be changed, or suppressed by the change in its immediate environment. It seems probable, therefore, that the non-deficient Notches in the class with normal chromosomes are caused by the suppression of the activity of the Notch due to the change in the gene, and that the majority of such Notches in the aberrant class are the result of the suppression of the activity caused by the position effect.

Unstable types

This group consists of the most interesting types available at present in the *Drosophila* material. These types are described in several regions of the chromosomal complex. They have been studied by a number of investigators, but there is still an appreciable amount of disagreement in regard to the interpretation of the various observations. In my collection thirty cases are available. This material is too large to be analysed here, and, therefore, only a few points which are of interest in connexion with the other material presented in this paper will be discussed in detail.

Unstable types show mottling of the mutant and wild-type tissues, which can be observed in males in the case of viable types and in heterozygous females in the case of lethals. All known loci of the white-Notch region may show mottling, namely, white, roughest, facet, diminutive, echinus and bifid. In the case of unstable white, larger or smaller red spots appear on either white or pale coloured background. A similar condition is found when other loci are involved.

In every one of the thirty cases of mottling a chromosomal rearrangement is involved, and in every case one of the breaks has occurred in the white-Notch region and the other in the heterochromatic region. The mottling, therefore, is induced in the loci of the white-Notch region when it is brought near to the heterochromatin. The relation between the heterochromatin and mottling was first shown by Schultz (1936), and the evidence obtained in this study supports his findings. There are, however, two cases in this collection where the transfer of the region to heterochromatin did not result in mottling. This indicates that although the heterochromatin is responsible for the mottling it does not induce it in every case.

Table 2. *The effect of the heterochromatin of various chromosomes on mottling in the white-Notch region*

Heterochromatin	Total	Mottled	Not mottled
X	5	3	2
2L	6	6	—
2R	6	6	—
3L	6	6	—
3R	3	3	—
4	6	6	—
	32	30	2

Table 2 gives the data showing the frequency with which the heterochromatin of various chromosomes participated in the changes of this group. It is evident from these data that the heterochromatin of every chromosome limb possesses the capacity of inducing mottling. The data also indicate that, with a possible exception of 3R, the heterochromatin of various autosomes is represented with the same frequency. Although these data are too small for establishing the lower frequency for 3R, they are sufficient to show that the heterochromatin of the *X*-chromosome is not as effective in inducing the mottling as the heterochromatin of the autosomes. As indicated in the mitotic chromosomes, the heterochromatin of the *X* is at least five times as long as the heterochromatin of the limb of an autosome, in spite of which the *X*-chromosome has been responsible for fewer cases of mottling than any other chromosome.

The data available in this collection indicate that certain regions of the heterochromatin are more effective in inducing mottling than other regions. This is evident from the material shown in Fig. 1. Types 264–29 and 264–55 are reciprocal translocations with one break in both cases between lines 3D4 and 3D5, and the other break is in the heterochromatin of 3L in one case and in the heterochromatin of 3R in the other. Type 264–29 shows mottling in *rst*, *fa*, and *dm* loci and 264–55 in *w*, *rst*, *fa* and *dm*. The next two types shown on the chart are also reciprocal translocations with euchromatin breaks at identical places and heterochromatin breaks in the same limb but not necessarily in the same position. Again there is a difference in the genetic effect between these two types. The two types next on the list show a similar difference in genetic behaviour. One of them, 264–12, shows mottling in the loci on both sides of the break, that is, in the region attached to the heterochromatin which remained near the spindle fibre as well as in the region of the heterochromatin carrying the distal part of the fourth chromosome. The other type, 258–18, showed mottling only in the loci attached to the spindle-fibre section of the heterochromatin.

The most convincing evidence for the differential effect of the heterochromatin is presented in the last

five types shown in Fig. 1. They are inversions or translocations in which the heterochromatin of the *X*-chromosome is involved. The first two of this group are inversions in which the break in the heterochromatin occurred to the right of the nucleolus-forming region (20C), so that the basal section of the heterochromatin carrying the spindle fibre became attached to the *dm-ec* section, and the distal section of the heterochromatin with the nucleolus-forming region came into contact with the *fa* to tip section.

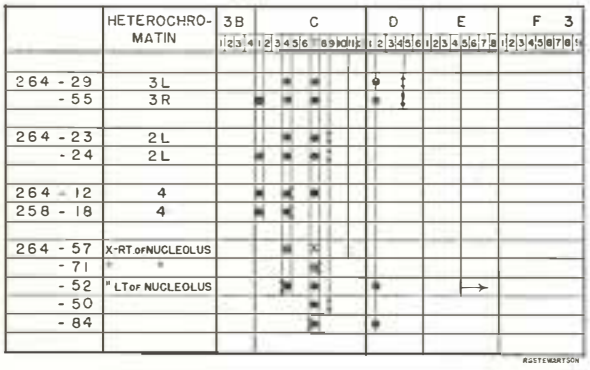

Fig. 1. Chart showing the breakage points in the white-Notch region, the type of the genetic effect observed near the break, and the heterochromatin involved in the rearrangement. In this and in the following figures letters and numbers in the first horizontal column refer to lines as shown on the Bridges' (1938) salivary gland chromosome map; vertical arrows indicate the position of breaks; a circle with a cross stands for stable changes not associated with a deficiency; a solid rectangle stands for deficiencies, a solid circle stands for unstable changes. The line 3C1 is taken to represent the white (*w*) locus, 3C4 roughest, 3C7 facet-Notch and 3D 1–2 diminutive. Echinus is to the right of 3F1–2 and bifid to the right of 4B4·5.

None of the loci showed mottling, but stable changes occurred in the tip section. On the other hand, 264–52 and 264–84 are similar inversions in which the break in the heterochromatin occurred to the left of the nucleolus-forming region. In both cases mottling was observed in the loci brought into proximity of the nucleolus-forming region which in these instances remained in the normal position at the base of the chromosome. Type 264–50 is a complex rearrangement in which the tip of the *X*-chromosome became attached to the *X*-heterochromatin with the break to the left of the nucleolus-forming region.

From these data it is evident that different regions of the heterochromatin differ in their potentiality of inducing mottling. It is also evident that the heterochromatin is more effective if attached to the spindle-fibre region, although there are three cases available in this collection where the mottling was induced by the section of the heterochromatin transferred from its normal position. The evidence indicates that the nucleolus-forming region of the *X*-chromosome has a high potentiality of inducing mottling, but only when it is located in its normal position near the spindle fibre.

Neither time nor space permits the discussion of the interpretation of mottling. It will suffice to say that a detailed study of the thirty cases representing this collection has strengthened my belief in the interpretation outlined in the joint paper with Mrs Slizyńska (Demerec and Slizyńska, 1937), namely, that genes of this region of the chromosome when brought into the proximity of the heterochromatin frequently become unstable. This instability may be due either to a reversible chemical change in the gene or may be caused by a reversible suppression of the activity of the gene.

The difference between the effects of heterochromatin and euchromatin

The effect of heterochromatin on the white-Notch region has already been described. It has two main characteristics: (1) it induces unstable changes, and (2) it may affect a number of adjacent loci, which effects may be separated from the point of attachment by a number of bands. This is shown in Fig. 2. Fig. 2 also gives the rearrangements where

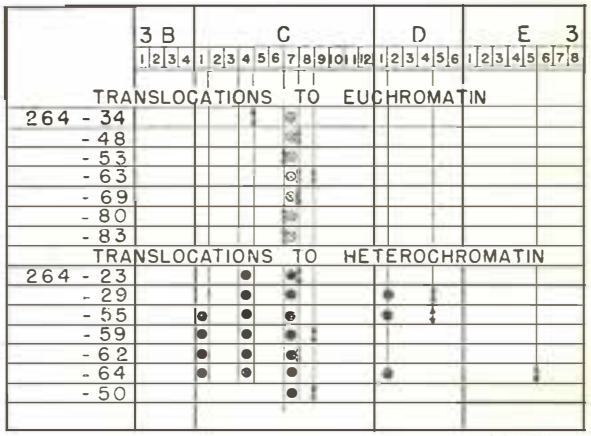

Fig. 2. A comparison between translocations to euchromatin and translocations to heterochromatin.

euchromatin is involved and shows a striking difference between the two groups. In the case of euchromatin rearrangements (1) only one locus very close to the break is affected, and (2) all changes are stable.

Origin of deficiencies

Thirty-three cytologically detectable deficiencies show from 1 to 50 bands missing. Now, a deficiency may be induced in one of two ways: (1) by two independent events, causing two breaks and a subsequent loss of a piece of a chromosome; and (2) by one event,

causing either two interdependent breaks with the loss of a piece or a chemical change. A study of the distribution of 1038 breaks made by Bauer, Demerec and Kaufmann (1938) showed that they are distributed at random, and, moreover, that the two breaks occurring in the same chromosome are independent of each other. From this it follows that if two independent events are responsible for a deficiency, it is to be expected that deficiencies of various lengths will occur with approximately equal frequencies. That holds true for large deficiencies involving more than 5 lines, but small, 1–5 lines, deficiencies are much more frequent than the expectancy. From a total of thirty-three deficiencies analysed here, nine are single-line deficiencies, two 2 lines, three 3 lines, two 4 lines, and one each of 5, 7, 11, 12, 14, 15, 18, 20, 22, 24, 25, 31, 35, 41, 44, 45 and 50 lines deficiencies. Thus, about one-half of the deficiencies (17) fall into the class of 1–5 lines and one-half (16) fall into the class of more than 5 lines. A glance at the distribution of various lengths shows that the difference in viability cannot account for the low frequency of large deficiencies. These data indicate that two mechanisms were instrumental in the production of these deficiencies, that is, the large and a part of the small deficiencies are induced by two independent events, and the majority of small deficiencies are induced by one event, either a chemical change, or two interdependent breaks.

Discussion

The material presented here is a good illustration of the complexity of the mutation problem. There is very little doubt that all changes mentioned above affect the genes in the white-Notch region in some way. It is also evident, however, that this effect differs in various cases. In certain types the effect is traceable to a physical loss of a piece of a chromosome, while in other cases an identical effect is produced by some other change which may or may not be related to a chromosomal rearrangement.

This work also brought out ample evidence to show the intimate relationship between the various parts of a chromosome. The evidence suggests that the activity of a gene depends greatly on its immediate environment. The activity of a gene may be changed or suppressed by chromosomal rearrangements through which a foreign section of a chromosome is brought into contact with the gene. It is evident that the various regions of a chromosome differ in the effect they produce. As shown by Kaufmann and Demerec (1937), the breaks in the euchromatic and the heterochromatic regions occur with an approximately equal frequency per length of the chromonemata. Since in *Drosophila* euchromatin is at least 3½ times as long as heterochromatin, it is to be expected that rearrangements involving the white-Notch section and a euchromatic region would be about 3·5 times as frequent as rearrangements involving heterochromatin. In the material used in the study, however, rearrangements involving heterochromatin are much more frequent than those involving euchromatin. Thirty-two were found in the first group and only nine in the second. Since these rearrangements are detected by the phenotypic effect they produce, this indicates that heterochromatin is much more effective than euchromatin in inducing changes in the white-Notch region. However, since the great majority of changes induced by heterochromatin are reversible and viable and those induced by euchromatin are stable and lethal, it may be said that in this particular region the heterochromatin produces a weaker effect than euchromatin.

In concluding it may again be stressed how sensitively balanced a living system is. The loss of a gene or even a change in a gene may greatly upset the normal functions of a cell, and just a mere rearrangement in the normal sequence of genes may upset or suppress the activity of a gene.

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Dobrovolskaia-Zavadskaia, N.A. ***Heredity and Environmental Factors in the Origin of Different Cancers***

In order to investigate the respective part of heredity and environmental factors in the origin of various cancers, it is necessary first of all to possess a reliable genetic material. The study of the heredity of cancer susceptibility, as carried out on *Mus musculus*, has yielded up to now only three particular forms approaching the simple Mendelian proportions, viz. leukaemia, lung cancer and epithelioma of the mammary gland.

A few years ago we had in our laboratory a strain of mice (strain III) which presented, in 20 % of the animals, lymphatic hyperplasia of the thymus, the spleen, lymph nodes, etc. (only now and then accompanied by blood changes). Our endeavours to increase

the frequency of this lymphatic condition in this particular strain and others all failed, and at present only rare sporadic cases break forth in our stock. We also had another strain (strain IV) with a certain tendency toward sarcomas (4·1 % in males and 14·3 % in females). We tried to increase their number by inbreeding from this strain IV, but failed even to maintain it. The cancer of the lung has appeared somewhat sporadically in different strains. Only the mammary epithelium has given a sufficient proportion of tumours to serve as a test for experimentation. Mammary epithelioma appeared in from 0 to 75 % of all females in fifty strains of our mice colony.

In order to investigate the environmental influences, we made use of various carcinogenic agents: chemical (tar, 1:2:5:6-dibenzanthracene), physical (radiant energy of radon), and living parasites (*Sp. morsus muris*). This paper is based on the observations derived from one cancerous strain (R III, 1184 animals) in which about 54 % of females died of mammary cancer, and five non-cancerous strains (XVII*nc*, XXX, XXXIX, XLI and XLII, 1547 animals), non-cancerous in the sense that no mammary cancer was found in control animals of the same strain.

In each of these strains, a certain proportion of animals reacted to the same irritant in a similar way, developing a squamous-cell epithelioma (very rarely a sarcoma) on the tarred spot, a sarcoma (very rarely a squamous-cell epithelioma) on the point of the dibenzanthracene injection, and a squamous-cell epithelioma or a sarcoma in the neighbourhood of a bare radon tube. In addition to these tumours, we found in certain females of strain R III some mammary epitheliomas in the regions of carcinogenic activity, but *more often* in other places. A comparative study of the topographic distribution of these tumours in treated and non-treated animals did not show any increase attributed to the carcinogenic activity. This failure of external factors to produce any glandular cancer, not only in non-cancerous but even in a high cancer strain, brings conclusive evidence that this form of malignancy is actually dependent on hereditary constitution. This assumption is reinforced by the extreme tenacity with which mammary tumours continue to develop not on the point of carcinogenic irritation, but on their habitual seats of origin, a manifestation of a localizing modifier.

On the contrary, sarcomas and squamous-cell epitheliomas appeared to depend pre-eminently on environmental factors. Although resistant individuals were numerous in all strains (long survival without cancerization), none even amongst the non-cancerous strains proved to be completely insusceptible to a tumour induced by a carcinogenic environment. Such extensive susceptibility to induced malignancy may be responsible for the usual appearance of tumours in the F_1 generation after crosses between representatives of cancerous and phenotypically non-cancerous strains. The corresponding genic factor is supposed to operate only in presence of a modifier for organic localization as regards the mammary epithelioma, or of some environmental stimulus in so far as sarcoma and squamous-cell epithelioma are concerned.

The role of "internal environment" (both genic and somatic) is discussed in connexion with the "normal overlaps" existing in high tumour strain R III. The search for methods by which a cancer-susceptible individual may be transformed into a normal overlap, opens new prospects for the prevention of cancer, if only in its mammary form.

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Dobzhansky, Th. ***On the Genetic Structure of Natural Populations of*** **Drosophila**

The theory of organic evolution has gained so general an acceptance that it seems an act of supererogation to remind biologists that evolution has been, in the main, not observed directly but inferred from a great body of morphological data. It is freely admitted that no change is noticeable in a vast majority of existing species over periods of the order of human lifetime. Situations like those in the domesticated animals and plants, and in a few wild species which have undergone some transformation in historical times are reputedly exceptional. Yet, according to the genetic theory, the pressure of the evolutionary factors, such as mutation, selection, isolation, and migration, is constant and unrelenting. A living species can hardly remain static for any length of time. It is a task of the investigator to observe evolutionary changes not only *post factum* but also *in statu nascendi*, in nature as well as under laboratory conditions.

Until recently studies on organic variation have been of necessity confined to observations on the morphological and physiological characteristics manifest in the phenotype. This variation is subject to a direct control by natural selection, and the freedom to change is therefore severely circumscribed. Any living species is precariously perched on its adaptive peak, and it must keep itself there on pain of extinction. The work of Chetverikov, Timoféeff-Ressovsky, Dubinin and his group, Gordon, Sturtevant, and others has, however, demonstrated the existence of a tremendous field of variation in the germplasm of sexually reproducing and cross-fertilizing species. This variation encompasses a wealth of mutant genes and of gene rearrangements. Most of the mutant genes are recessive and sufficiently rare, so that they seldom

manifest themselves in the phenotype of the homozygotes. The gene rearrangements are chiefly inversions, which, except where position effects are produced, have no influence whatever on the phenotype. Although from the standpoint of a systematist or a morphologist this concealed variation is potential rather than one actually available to the species, it obviously represents the store of the evolutionary raw materials, from which evolutionary changes must spring if they are to occur at all. This hidden field of variation, detectable not through observations on the phenotype but only by genetic and cytological means, must engage the attention of students of evolutionary mechanisms.

For the past few years a group of workers at Pasadena has attempted to determine the extent of the concealed genetic variation in the species *Drosophila pseudoobscura*, to estimate the magnitude, and to understand the manner of interaction of the factors that mould the genetic composition of the natural populations of this species. The gene arrangement in the chromosomes proved to be remarkably inconstant. Sturtevant and the writer have described seventeen arrangements in the third chromosome of this species, and two more have been found since. Practically all gene arrangements are related to each other as overlapping inversions, which fact has permitted uncovering the phylogenetic relationships of these structures. In most parts of the geographic area inhabited by this species the wild populations are mixtures of several, up to six, gene arrangements. Individuals homozygous and heterozygous for the different arrangements occur in relative frequencies demonstrating that the populations are panmictic ones. Appearance of an inversion certainly does not split the species in two non-interbreeding parts. Each gene arrangement is restricted geographically to a definite territory. Some are distributed very widely, while others are endemic; in general, groups of phylogenetically related forms occur together, although some oddly discontinuous geographic areas are observed; in some parts of the species territory the population is highly diversified (e.g. in Mexico, California, central Rocky Mountains), while in others it is more uniform (e.g. in Utah, Arizona, New Mexico and Colorado). All these relations seem to shed light on the history of the species, of its distribution and migrations, but no place can be spared here to discuss these aspects of the situation. The chromosomes other than the third are likewise variable, but to a much smaller extent.

An analysis of the gene contents of the wild third chromosomes has been made by means of a genetic technique that permits the obtaining of individuals known to be homozygous for individual chromosomes sampled from natural populations. The results of this work may be summarized as follows. While not so long ago certain authors doubted that mutants ever occur outside of genetic laboratories, one must now come to the conclusion that certainly more than half of the individuals of *D. pseudoobscura* found outdoors are heterozygous for one or more mutant genes. Indeed, from 14 to 34 % of the third chromosomes carry recessive lethals and semilethals. Genes deleterious to the viability of the carrier, but having effects not sufficiently strong to be classed as semilethals, are very common. It is difficult to determine exactly the frequency of the chromosomes with such deleterious modifiers, but the estimate of 40 % does not seem too high. It is also difficult to make an exact census of chromosomes containing mutant genes with visible external effects; approximately 2 % of the third chromosomes have mutant genes comparable to those used in laboratory experiments involving linkage or similar problems. Finally, genes modifying the duration of the development of the fly, both retarding and accelerating it, as well as genes making one or both sexes sterile, are abundant in natural populations.

Owing to their detection being easy and accurate, the lethals and semilethals are an especially favourable material for population studies. The equilibrium frequency of a recessive lethal, i.e. the frequency to which it is allowed to accumulate in a population, is the square root of the frequency of its *de novo* origin by mutation. Provided the mutation rates are alike, and provided the effective sizes of the breeding populations are sufficiently large, all populations of a species should carry equal concentrations of lethals. This is not the case in *D. pseudoobscura*. In populations inhabiting the mountain ranges of the Death Valley region of California and Nevada $14{\cdot}96 \pm 0{\cdot}82$ % of the third chromosomes carry lethals and semilethals, while the corresponding figure for Mexico and Guatemala is $30{\cdot}00 \pm 2{\cdot}82$ %. The mutation rate must be four times greater in Mexico and Guatemala than it is in Death Valley to account for the observed difference in the concentration of lethals. Experiments were arranged in the laboratory to test this possibility. In the material of Death Valley origin forty lethal mutations were detected in 13,472 chromosome generations, while in the Mexican and Guatemalan material 7699 chromosome generations gave twenty-five lethals. The mutation rates, $0{\cdot}297 \pm 0{\cdot}032$ and $0{\cdot}325 \pm 0{\cdot}044$, are not significantly different, and certainly one of them is not four times greater than the other. It follows that at least in the Death Valley region the effective size of the breeding population is limited. Not only the species as whole, but even parts of it inhabiting rather small portions of its total geographic area, do not represent elementary breeding units. Such units must be groups of individuals in-

habiting very small territories, and the species as a whole is the sum total of a very large number of these units. The truth of this proposition may be demonstrated in a variety of ways.

Since about 15 % of the wild third chromosomes carry lethals (in Death Valley region), about 2·25 % of the zygotes formed in natural populations receive a lethal from each of the two parents. Evidently, such zygotes are inviable if the two lethals are allelic. The frequency of alleles was studied in a sample of 123 lethals recovered from eleven population samples from as many different localities in the Death Valley region. Every lethal was tested by crossing the strain carrying it to practically every one of the remaining 122 strains. The experiment was subdivided into two parts: first, lethals encountered in the same population were intercrossed, and, second, lethals from different localities were tested. Among the intra-locality crosses, $3{\cdot}11 \pm 0{\cdot}42$ % (24 out of 772) carried allelic lethals, while among the inter-locality ones the frequency of alleles amounted to only $0{\cdot}366 \pm 0{\cdot}055$ % (20 out of 5460). It should be borne in mind that the localities in which these lethals were detected are isolated from each other by stretches of the territory where the species apparently does not live. This raises a strong presumption that the allelic lethals found in the different localities are independent in origin, while those in the same locality may be derived from a single original mutation. It follows that the frequencies of some of the lethals may increase within a population. For example, one of the lethals has been found four times among fifty-five tested chromosomes from one of the localities, counting the chromosomes that carried lethals as well as those free of them. This is a very high concentration for a lethal. Most of the lethals found more than once in a given population have not been recovered at all in populations from other localities. This fact excludes the possibility that the lethals encountered several times in certain populations are those that arise by mutation more frequently than lethals at other loci. The phenomenon of the accumulation of lethals shows that the effective breeding sizes of the populations studied are small enough to permit considerable random fluctuation of the gene frequencies to take place.

The frequency of the zygotes dying on account of the homozygosis for lethals is a product of the frequency of the zygotes carrying two lethals (2·25 %) and that of the allelic lethals among the latter (3 %). By multiplication we obtain the figure 0·067 %, which, consequently, represents the rate of the elimination of lethals in natural populations. In any population at equilibrium, the elimination rate of the lethals must be equal to the rate of their *de novo* origin by mutation. As shown above, the mutation rate is approximately 0·3 %, or between four and five times greater than the calculated elimination rate. This glaring discrepancy certainly requires an explanation. Several possibilities may be suggested. It may be noted, for example, that all the computations are based on the assumption that both the lethals found in natural populations and those obtained in experiments are completely recessive. If some of the lethals produce semi-dominant deleterious effects, their elimination may take place in the heterozygous, as well as in the homozygous, condition. Experiments, the detail of which must be omitted here, were arranged to test this possibility. Although the results were consistently negative, the existence of very slight dominant effects in some lethals is not out of the question. Another possibility is that at certain seasons the fly populations are reduced, due to unfavourable conditions, to so few individuals that there takes place much inbreeding of close relatives, and with it a more rapid elimination of lethals than is the case at seasons when *D. pseudoobscura* is more abundant. Finally, our population samples were taken in such a manner that some of the flies were collected at a distance up to half a mile from others. If the flies spend their lives within the immediate vicinity of the places where they develop, the population may be differentiated into colonies so small that our samples do not represent panmictic groups. Work designed to secure more information on this point is in progress.

The number of the loci in the third chromosome which can, by mutation, give rise to lethals is an important constant for various calculations. An attempt was made to estimate the order of magnitude of this constant. On the assumption that lethals found in populations inhabiting different isolated localities are independent in origin, the frequency of the occurrence of allelic lethals in a sample of a given size is a function of the total number of loci producing such lethals. A sample of 105 lethals contained 68 lethals once, 17 twice, and 1 lethal three times. With the aid of formulae devised by Profs. Sewall Wright, Morgan Ward, and H.J. Muller, whose courtesy must be here acknowledged, the number of the loci producing lethals in the third chromosome turns out to be approximately 250. Two reservations must be made in this connexion. First, the assumption is implicit in the calculations that all the loci mutate toward lethality equally frequently. If, as seems entirely possible, some loci are more mutable than others, the figure 250 is an underestimate. Second, the number of the "loci" so calculated is not necessarily the same as the total number of the genes borne in the third chromosome of *D. pseudoobscura*. If, for example, the lethals represent not point mutations but short deficiencies, the value obtained indicates that the average length of such a deficiency is about $\frac{1}{250}$th of the length of the chromosome.

Since the total frequency of mutations producing lethals in the third chromosome is 0·3 % per generation, the frequency per locus is approximately 0·00122 %, or 1:81,425. In very large populations the equilibrium frequency for each lethal equals the square root of the mutation rate, or 0·349 %. The greatest actually observed concentration of all lethals in a wild population is 34·21 ± 5·20 % of the third chromosomes (in Guatemala), which indicates an average concentration per locus in the neighbourhood of 0·137 %, or only a little more than a third of what is expected in a very large population. The conclusion follows that the effective sizes of all the populations of *D. pseudoobscura* so far examined are very small. Comparisons of the theoretical and the experimentally established concentrations of lethals permit, in fact, the estimation of the numerical value of the population size, the *N* of Sewall Wright's formulae. Such computations are premature at present, since several sources of error may vitiate them. It has been pointed out already that some of the lethals may not be completely recessive, and that during certain parts of the seasonal cycle the elimination rate of lethals may be high due to local inbreeding. It should be emphasized, however, that the most dubious of all the assumptions which we have been forced to make, namely, that of the equal mutation rates for all lethals, will not, even if proven wrong, invalidate the conclusion that the population size in *D. pseudoobscura* is small. Indeed, if the number of the lethal-producing loci in the third chromosome is higher than 250, the concentrations of the lethals in very large populations must be even more different from the actually observed ones than inferred above.

In a species broken up into a large number of semi-isolated colonies, each with a small effective size, certain genetic phenomena are expected. In the first place, populations inhabiting closely adjacent localities may sometimes be different in constitution, and, secondly, the composition of each population may fluctuate widely in the course of time. It has already been pointed out that the lethal contents are different in the populations from various localities in the Death Valley region. Even more convincing is the evidence derived from comparisons of the relative frequencies of the gene arrangements in the third chromosome in different populations. Dobzhansky and Queal have shown that among the eleven mountain ranges in the Death Valley region where population samples were taken, only three ranges are similar. The populations inhabiting the remaining eight ranges all differ from each other to a greater or lesser extent. Dr P. Ch. Koller found that population samples taken in localities only a few miles distant on the same mountain range show about as great a diversification as do the samples from the different ranges. Apparently significant differences have been observed also between population samples taken by Prof. J.T. Patterson in places only about two miles apart in southern Texas. This is of interest because fewer secular isolating barriers are available on the rolling plains of Texas than in the extremely rugged terrain of the Death Valley mountains.

Temporal changes in the composition of the same population have also been recorded. A single example of this phenomenon will suffice here. Population samples were taken in Wildrose Canyon, California, by Dr P. Ch. Koller and the writer on three successive years. Table 1 summarizes the results.

Table 1. *Frequencies (per cent) of the gene arrangements in the third chromosome in a population of* Drosophila pseudoobscura

Date of collecting	Gene arrangements: Standard	Arrowhead	Chiricahua	All others	Chromosomes examined
20 May 1937	13·8	67·4	18·8	—	224
27 May 1938	34·0	37·8	25·0	3·2	156
25 Sept. 1938	31·1	41·9	18·9	8·1	74
10 June 1939	35·3	45·8	15·3	3·7	190

The same three gene arrangements, namely, Standard, Arrowhead, and Chiricahua, were the commonest at all times. Their relative frequencies underwent, however, a pronounced change between May 1937 and May 1938. Since then this population has remained more or less stationary, or perhaps has shown a slight drift back toward the 1937 condition. Experiments now in progress should bring further information about the temporal changes in various populations.

The species, *D. pseudoobscura*, is a dynamic system of local colonies which can pursue, within certain limits, independent evolutionary courses. Elementary evolutionary changes do not involve the species as a whole, or even any large subdivision thereof which could be justifiably called a "race". They take place in colonies whose effective breeding sizes are so small as to permit perceptible random fluctuations in the genetic constitution. Only secondarily, through migration and selection of superior genotypes formed in such colonies, can the texture of the species as a whole become gradually altered.

The question immediately presents itself as to how widely these conceptions of the genetic structure of a species and of its evolution are applicable to forms of life other than *D. pseudoobscura*. This can be decided, of course, only by future investigations. Nevertheless, it is already sufficiently clear that evolutionary situations are not identical in all species. The groups where asexual reproduction, or self-fertilization, or poly-

ploidy occur should not be confused with species of *Drosophila*. Even among the obligatorily cross-fertilizing types the effective breeding sizes of the populations may be very different, depending upon the abundance of the species and the range of activity of individuals. It is very probable that evolutionary changes differ both in rate and in kind in very common and mobile species on the one hand, and in rare and more sedentary ones on the other. Perhaps the greatest biological change effected by civilization is the alteration of the evolutionary pattern of mankind, from that of a species segregated into numerous semi-isolated colonies with medium or small effective population sizes to that of an immense population with subdivisions that are no longer genetically operative.

72

DONALD, H.P. ***Genetic Aspects of Growth Rate in Bacon Pigs***

Genetic studies of growth may be divided into three broad groups. Pre-natal growth, which has a survival value and probably also an influence on post-natal development, appears to be subject more to maternal control than to foetal genetic constitution. Whereas in pigs the sire would seem to exert very little influence on birth weight, dams are characterized by a fairly consistent average weight of progeny. Birth weight may therefore be more a character of the dams than of the offspring. Similarly, growth up to weaning age is largely determined by the milk production of sows. Genetic variation in this character on a large scale has to be inferred from a large amount of practical experience rather than from critical experiments.

There is much evidence to show that the progeny of different sires and dams vary in their rate of growth, but it is extremely difficult to determine how much is genetic in origin. Data from established breeding herds of pigs are given to show that there is a strong tendency among breeders to introduce consistently and frequently the best available outside blood. This would seem to diminish the possibility of finding numerous well-defined strains within the breed which might differ in rate and economy of gain, and to increase the adaptability of the breeds as a whole to changes in ideal type. Doubts are cast on the advisability of perfecting environmental conditions for litter-testing purposes, for although this might permit the most effective test of genetic potentiality for growth, it would detract from the value of the tests for showing up litters superior in respect of economy of gain, and hardiness, which are important under commercial feeding conditions.

73

DRY, F.W. ***Kemp in the New Zealand Romney***

The abundance of halo-hairs (large birthcoat kemps) generally depends on multiple factors. In two stocks on the Massey College Farm, very high abundance of halo-hairs is determined by a single dominant factor, linked with the sex-influenced factor for horns with a cross-over value of about 10 %. This definite Mendelian factor sometimes is expressed incompletely, producing many halo-hairs only, as distinct from very many.

Genetic factors (unanalysed) are important in determining whether or not kemp continues to grow after the original birthcoat kemps have fallen out. A certain amount of attention has been paid to differences between animals in the nature of the immediate successors of birthcoat kemps, and to differences in the nature of their successors grown late in the first fleece.

The inheritance of fibre-type array is pertinent to the inheritance of kemp. Fibre-type array (on standard back position) is strongly inherited. When the array (notably Valley) is indicative of an intense pre-natal check, then kemp rarely grows in any abundance late in the first fleece, even though it has been plentiful earlier. In order that kemp should be grown in abundance late in the first year, not only must kemp be present earlier, but the array is almost always one (notably Saddle) indicative of a weak pre-natal check. The conclusion just presented shows the bearing upon a practical question of detailed "hair-splitting".

74

DUNLOP, G. and WILLIAMS, S. ***Controlled Feeding Techniques for Measuring Genetical Differences***

Material used for investigations on inherited characters of economic importance (such as rate of growth and conformation) has consisted largely of observational data on individuals subjected to different environmental treatments. Much of the variation found amongst animals can be accounted for by uncontrolled group feeding and seasonal influences. In this paper standardized and controlled feeding techniques are outlined. These would appear to have a special application for State Breeding Farms and Litter Testing Stations.

To compare animals of different genetic constitution and their offspring over a number of generations, the environment must be controlled as strictly as possible. Environment has reference to (1) Management, (2) Housing, (3) Nutrition.

(1) *Management.* The dams of the offspring on

which observations are to be made should be kept under standard and optimal conditions, at least during pregnancy. The young should be removed from the mother as early as possible, preferably after the first day of life, and submitted to controlled feeding. In this way many early post-natal environmental influences are equalized, and differences in genetical make-up have a greater chance of making themselves apparent.

(2) *Housing*. Temperature of the surroundings must be controlled and should be maintained well above the critical temperature of the animals, say 63° F. or other optimal temperature, in conjunction with a low humidity throughout all seasons of the year. Methods of control of environmental conditions are suggested.

(3) *Nutrition*. To ensure uniformity in the nutrition of the animals, a standard and complete ration must be devised, the constituent foodstuffs being freely available at all seasons of the year and over a number of years. The ration must be fed in amounts strictly according to the live weight of the animal. For the production of young, milk or eggs, an extra allowance of food must be graduated according to a fixed scale depending on the daily level of production of the individual.

The superiority of the individual controlled feeding method over uncontrolled group-feeding methods is stressed, both methods having been used in pig experiments conducted at Cambridge and the Midland Agricultural College. Results of trials comparing the growth rates of a number of litters are presented. It is to be noted that gilts grow significantly faster than hogs, reaching 60 lb. live weight for a period of considerable duration when subjected to individual controlled feeding.

75

EATON, O.N. ***The Effect of Crossing Inbred Lines of Guinea-pigs upon the Characteristics of the Hybrids***

All possible crosses were made among five strains of guinea-pigs which had been inbred, brother to sister, from ten to thirty generations. The hybrids were compared with one another, with the parent strains, and with a non-inbred control stock in various measures of fertility, growth, and mortality. No single inbred strain excelled any other in all measures of these three factors. A cross between the two families ranking second and last in fertility gave an F_1 ranking first in this character, while a cross between families ranking first and third gave the lowest fertility in F_1. These same crosses produced the best and poorest growth results also. Two families with the lowest mortality produced an F_1 with high mortality. Hybrids from two families showing the greatest growth were not so heavy at maturity as those from some of the lighter parent strains. The F_2 generation in general followed the same rank as the F_1. Thus, two of the best F_2 hybrids came from the same inbred strains which produced two of the best F_1 hybrids. Similarly, two of the poorest F_2 hybrids came from the same parent families as two of the poorest F_1 hybrids. Differences in the characteristics, particularly growth, of the F_1 progeny from reciprocal crosses were noted in certain cases, this being due primarily to the influence of the dam upon the characteristics of the young. All the inbred families were inferior to their F_1 hybrids, whereas the control stock excelled both inbreds and hybrids in the characters compared.

76

EDWARDS, J. and WALTON, A. ***Problems of Semen Production related to Artificial Insemination***

Since the contribution which the technique of artificial insemination has to make to livestock improvement lies in the greater use that can be made of sires of known genetic merit, it is clear that factors controlling the fertility of such sires (the rate of production and the quality of their semen) are of great importance. The usefulness of a prepotent sire is determined by his ability to maintain a high rate of sperm production and to produce spermatozoa of a quality that will survive storage and transport.

The paper deals with variations in qualities and quantity of spermatozoa in a group of fifteen bulls examined over a period of one year. Factors influencing the quality of the ejaculates, and the relation between the "respiration rate" of the spermatozoa and their fertilizing and storage properties are discussed. The need of a standard test for the rate of sperm production and a test that will relate the vitality of the spermatozoa to their fertilizing capacity in a herd of normal females is emphasized. Both are essential for the successful practice of artificial insemination, as standards for experimental work on factors governing sperm production, and for the proper exploitation of sires of superior genetic constitution.

77

ELLISON, W. ***The Cytology of Certain Diploid and Tetraploid*** **Avena** ***Hybrids***

DIPLOID PLANTS, $2n=14$

The cytology of several diploid *Avena* hybrids has been studied as well as that of the parental species.

One parent, an unidentified species with articulated grains and designated Cc 1795, was used in many of these crosses. A cytological examination of this plant revealed two significant features, namely that pairing was good at the first metaphase of meiosis and meiosis as a whole proceeded regularly, secondly in the anthers from some plants through the failure of the necessary cell-wall formation, giant pollen mother cells were formed which had 14, 21 and 28, or even more bivalents. Quadrivalent associations were not seen during meiosis in this species.

In the other parental species *A. brevis*, *A. strigosa*, *A. weistii* and *A. strigosa* subsp. *hirtula*, meiosis proceeded normally and resulted in good pollen formation. During meiosis in the F_1 plants obtained by crossing *A. brevis* and *A. weistii* with Cc 1795 a single quadrivalent ring was observed in each pollen mother cell at the first metaphase. This quadrivalent ring was orientated either disjunctionally or non-disjunctionally in the ratio of 2:1 on the first meiotic metaphase plate in both F_1 plants.

An analysis of the pollen of these hybrid plants indicated that approximately 35 % was abortive. From the progeny of *A. brevis* × Cc 1795 two segregates, which were homozygous for two base types indicated by *X* and *Y*, were crossed together. The cytological behaviour of this hybrid was practically the same as that of the two F_1 plants mentioned above.

In hybrids obtained by intercrossing any of the diploid species *A. brevis*, *A. weistii*, *A. strigosa*, or *A. strigosa* subsp. *hirtula*, meiosis was normal in that seven bivalents were always present at the first metaphase and both meiotic divisions proceeded regularly. One point of interest was observed in the F_1 plants from the cross between *A. brevis* and *A. strigosa* subsp. *hirtula*. From observations made at late pachytene and diakinesis one of the bivalents appears to consist of a pair of chromosomes of unequal length.

TETRAPLOID PLANTS, $2n=28$

These F_1 plants were derived from crosses between *A. barbata* and *A. Abyssinica*. In both parents meiosis was normal and bivalents only were found during the first meiotic division. In the hybrid plants one quadrivalent ring was a characteristic feature of each pollen mother cell and, as in the diploids, the quadrivalent ring was orientated at the first metaphase either disjunctionally or non-disjunctionally in the ratio of 2: 1. Approximately 33 % sterility has been found in the F_1 plants.

The occurrence of the quadrivalent rings in some of the diploid and the tetraploid hybrid plants indicates that such plants are structural hybrids.

78

EMERSON, S. ***The Distribution of Self-sterility Allelomorphs in a Natural Population***

Oenothera organensis has certain inherent peculiarities which suggest it as favourable material for a study of population genetics: (1) the species is endemic to a small mountain range, occupying an area of less than 50 square miles, where it occurs in isolated groups in the various canyons; (2) the population is extremely small, there are probably less than 1000 individuals, offering the possibility of analysing the entire population; (3) the species is self-sterile, making cross-pollination obligatory; (4) the self-sterility is governed genetically by a series of at least forty allelomorphs which can be followed throughout the population. The report will be on the completed analysis of a sample of over 100 plants collected in 1937. A partial analysis of this material has given indications that: (1) the entire population forms a single, more-or-less closely interbreeding unit; (2) seed dispersal probably occurs chiefly through the agency of water and in a down-stream direction; (3) the transfer of allelomorphs between canyons is probably accomplished through the pollen; (4) most flowers are pollinated by a mixture of pollen from several other plants. The completed analysis should offer additional information relative to these points as well as giving some idea of the relative frequencies and distributions of the different allelomorphs.

79

EPHRUSSI, B., VOGT, M. et GOLDSTEIN, L. ***Sur la relation entre la production de l'hormone*** v^+ ***et le dosage du gène*** v^+ ***chez*** **Drosophila melanogaster**

Dans ces dernières années, plusieurs cas ont été décrits où les gènes se manifestent par l'intermédiaire de substances de nature hormonale. Le nombre de caractères mendéliens non-autonomes connus s'est ainsi considérablement accrû et ce qu'on considérait, il n'y a pas longtemps, comme des cas tout à fait exceptionnels, sans être devenu la règle, peut être regardé aujourd'hui comme type d'action génique: il n'y a aucune raison d'admettre que les processus qui déterminent la différenciation d'un caractère autonome et qui se déroulent à l'intérieur de la cellule, soient fondamentalement différents de ceux qui, comportant la formation d'un "messager chimique", provoquent une différenciation à distance. La différence entre les deux cas peut se réduire éventuellement, comme l'a suggéré Haldane (1938), à des conditions purement mécaniques, telles que la grandeur moléculaire de la substance active.

Nous allons donc considérer les facteurs hormonaux intervenant dans la réalisation des caractères mendéliens comme des chaisnons intermédiaires typiques de la chaîne de réactions reliant les gènes aux caractères. Les problèmes qui se posent à partir de ce moment sont ceux des relations entre ces facteurs hormonaux et les caractères, d'une part; et entre les facteurs hormonaux et les gènes, d'autre part. Le premier problème ne sera pas discuté ici: le deuxième, qui n'est qu'une partie du problème général du mode de formation des produits de l'activité des gènes, est celui qui nous a conduit à entreprendre les recherches dont il sera question. La première question à résoudre est celle de savoir si les facteurs hormonaux sont des produits immédiats de l'activité génique ou si, au contraire, il y a d'autres chaînons intermédiaires entre ces facteurs hormonaux et les gènes qui contrôlent leur formation.

Disons tout de suite que des considérations *a priori* conduisent souvent à l'impression que les relations entre les gènes et les facteurs hormonaux ne sont pas simples. Dans le cas, par exemple, de l'hormone de floraison découverte par Melchers (1937) il a été montré que la production de l'hormone peut être provoquée prématurement chez les plantes biennales par l'action du froid. De même, dans le cas de l'hormone v^+ de la *Drosophile*, il a été montré par Khouvine, Ephrussi et Chevais (1938) que les animaux de la race *v* (*vermilion*), caractérisés par une déficience en hormone, peuvent être induits à en produire par l'action du jeûne. La production de l'hormone semble donc être intimement liée au métabolisme de la mouche. Ces observations mènent à l'impression d'une relation très indirecte entre les gènes et les substances dont ils contrôlent la formation. Il est évident cependant que ces indications sont insuffisantes pour trancher la question.

Les difficultés que rencontre la solution de ce problème sont trop connues pour que nous y revenions ici. Nous dirons simplement qu'avec un certain nombre d'auteurs nous croyons que l'étude quantitative de l'effet du dosage des gènes sur leur manifestation phénotypique pourrait être une des voies d'approche les plus fructueuses et nous rappelons particulièrement à cet endroit l'article de S. Wright (1934) où sont discutées les implications et conséquences théoriques de ce genre d'études. Le cas des hormones de la coloration des yeux de la *Drosophile* nous a paru mériter particulièrement une telle analyse, parce que l'autre partie du problème—la relation entre le facteur hormonal et le phénotype—ne semble pas devoir, dans ce cas, rencontrer de difficultés spéciales; et parce que, d'autre part, comme on le verra bientôt, la substance active peut, dès à présent, être dosée avec une précision souvent suffisante.

Dans ce qui suit, nous donnerons les premiers résultats de ce travail qui, dans cette première phase, a pour objet limité la question suivante: *La quantité d'hormone v^+ formée par un implant, dépend-elle, et dans quelle mesure, du dosage du gène v^+?*

Production différente d'hormone par les implants ♂ et ♀

On se souvient que l'hormone v^+ est une substance nécessaire à la formation du pigment du type sauvage. Son absence caractérise le mutant *v* qui, lorsqu'on lui injecte l'hormone v^+, réagit par la formation d'une pigmentation identique à celle du type sauvage.

Le gène *v* est lié au sexe; les ♀♀ en portent deux doses, tandis que les ♂♂ n'en portent qu'une. Si la quantité d'hormone produite dépendait du dosage du gène v^+, on devrait donc trouver que les organes producteurs d'hormone en forment plus chez les ♀♀ que chez les ♂♂. Ceci peut être vérifié expérimentalement par l'implantation d'yeux de ♀♀ ou de ♂♂ de certains mutants, dans des hôtes réactifs, tels que *vermilion-brown* (*v*; *bw*): les yeux des hôtes devraient former, sous l'influence des implants prélevés sur des donneurs ♀♀, plus de pigment. Le "foncement" des yeux des hôtes peut être évalué numériquement par comparaison avec une échelle d'étalons établie par Tatum et Beadle (1938): celle-ci est constituée par des mouches de neuf génotypes différents, formant une série d'intensités de coloration, auxquelles sont attribuées des notes (indices de couleur) allant de 0 à 5 (le 0 correspondant yeux blancs aux des mouches *v bw* et le 5 aux yeux du mutant *bw*).

Nous avons implanté des yeux du mutant *white* (*w*) dans des hôtes *v bw* ♂. Nos observations, portant sur 254 implants ♂ et 258 implants ♀, nous ont fourni les moyennes suivantes:

$$♂♂ = 0{\cdot}71 \pm 0{\cdot}01, \quad ♀♀ = 1{\cdot}16 \pm 0{\cdot}02.$$

La différence entre les deux valeurs ($0{\cdot}45 \pm 0{\cdot}02$) est, on le voit, 22 fois l'erreur standard, donc statistiquement assurée.*

Origine de la différence

Telles quelles, ces expériences ne permettent cependant pas de distinguer si l'activité plus grande des disques ♀♀ est due à la double dose des gènes v^+, au dosage d'autres gènes du chromosome *X* ou, enfin, au sexe des implants. Cette question sera résolue par les expériences suivantes, où l'on tiendra compte de la relation simple qui existe entre production (*P*),

* La mesure d'un grand nombre d'implants ♀ et ♂ ne nous a pas révélé de différence de taille.

utilisation (U) et libération (L), relation établie par Ephrussi et Chevais (1938) et qui peut s'écrire

$$L = P - U^*.$$

Cette relation montre en outre que l'utilisation de l'hormone est proportionnelle à la pigmentation des implants. Considérons les yeux des mutants *w*, w^a, w^e et w^{co}. La pigmentation des deux premiers ne montre pas de dimorphisme sexuel; chez les deux autres, au contraire, les yeux des ♀♀ sont beaucoup plus pigmentés que les yeux des ♂♂. L'utilisation de l'hormone par les yeux ♀♀ et ♂♂ sera donc égale dans les cas des implants *w* et w^a tandis que, dans les cas de w^e et w^{co}, elle sera plus forte dans les yeux des ♀♀ que dans ceux des ♂♂. Considérons encore les ♀♀ des mêmes mutants hétérozygotes pour *v*; leur pigmentation est, dans tous les cas, identique à celle des ♀♀ homozygotes pour v^+: l'utilisation d'hormone sera donc aussi pareille à celle des ♀♀ homozygotes pour v^+. Le tableau 1 montre ce que doit être la libération de l'hormone par les différents mutants considérés, selon (A) l'hypothèse de l'indépendance de la production de l'hormone du dosage du gène v^+; (B) l'hypothèse de la dépendance de cette production soit du sexe des implants, soit du dosage d'autres gènes du chromosome *X*; (C) l'hypothèse de la dépendance de la production de l'hormone du dosage du gène v^+.

Les résultats expérimentaux s'accordent nettement avec l'hypothèse (C). Les résultats des implantations des yeux de tous ces mutants hétérozygotes pour *v* sont particulièrement convaincants. Nous pouvons donc considérer comme établi que, dans les limites examinées jusqu'ici, la production d'hormone v^+ augmente avec le dosage du gène v^+.

* Notons en passant que cette règle comporte quelques exceptions, dont nous n'avons pas à tenir compte ici. Les yeux *w* ne formant pas de pigment, nous supposons que $U=0$; on peut admettre alors que $L=P$. Il est à noter ici que dans toutes ces expériences nous ne tenons pas compte de l'hormone cn^+ qui est simultanément libérée par les implants.

Les chiffres suivants montrent que lorsque la libération d'hormone est causée par des gènes autres que ceux de la série *w*, qu'il s'agisse de gènes liés au sexe ou autosomaux, cette libération est de même plus grande pour des implants ♀♀ que pour des implants ♂♂.

Mutant	Sexe de l'implant ♀	♂
g^2	0·76 ±0·01	0·35 ±0·01
st	1·38 ±0·04	0·84 ±0·03
cn	1·99 ±0·06	1·32 ±0·03
lt	0·92 ±0·03	0·56 ±0·02

Notons maintenant que, ne connaissant pas les quantités de pigment qui correspondent aux différents indices de couleur, nous ne pouvons pas déduire de ceux-ci les quantités d'hormone correspondantes et, par conséquent, calculer le rapport: 2 doses/1 dose. On voit donc l'intérêt qu'il y aurait à établir la relation entre les indices de couleur et les quantités d'hormone.

Tableau 1. *Libération de l'hormone v^+ par les yeux des mutants w, w^a, w^e, et w^{co} implantés dans des hôtes v bw ♂*

(♀, 2 doses du gène v^+; ♂, 1 dose; *h*, ♀ hétérozygote pour *v*.)

	W, W^a (Pigment ♀ = Pigment ♂)	W^e, W^{co} (Pigment ♀ > Pigment ♂)
	$U_♀ = U_♂ = U_h$	$U_♀ - U_h > U_♂$
Hypothèse A $P_♀ = P_♂ = P_h$	$L_♀ = L_♂ = L_h$	$L_♀ = L_h \ll L_♂$
Hypothèse B $P_♀ = P_h > P_♂$	$L_♀ = L_h > L_♂$	$L_♀ = L_h \gtrsim L_♂$
Hypothèse C $P_♀ > P_♂ = P_h$	$L_♀ > L_♂ = L_h$	$L_♀ \gtrsim L_♂ > L_h$
Observ.	*w* : ♀ = 1·20 ±0·04 ♂ = 0·73 ±0·03 *h* = 0·67 ±0·03 w^a: ♀ = 1·48 ±0·05 ♂ = 0·74 ±0·04 *h* = 0·83 ±0·03	w^e: ♀ = 0·95 ±0·04 ♂ = 0·64 ±0·03 *h* = 0·46 ±0·02 w^{co}: ♀ = 0·62 ±0·04 ♂ = 0·36 ±0·02

Essai d'analyse quantitative

La conversion des indices de couleur de l'échelle de Tatum et Beadle en unités conventionnelles d'hormone a été opérée par ces auteurs de la manière suivante: une série de dilutions différentes d'un même extrait riche en substance v^+ sont injectées à des larves *v bw*. Les mouches écloses sont étalonnées par comparaison avec l'échelle déjà décrite et la valeur maxima de l'effet observé pour chaque concentration est notée. On obtient ainsi une courbe reliant l'effet à la concentration relative d'hormone. Si on prend comme unité conventionnelle d'hormone la concentration qui donne l'indice 1, on trouve une relation linéaire entre l'indice de couleur et le logarithme de la concentration.

Nous pouvons naturellement traduire les indices de couleur que nous venons de trouver, en unités conventionnelles d'hormone d'après cette même

courbe de Tatum et Beadle; nous trouvons ainsi pour les implants *w* les valeurs

$$\text{♀} = 1{\cdot}23 \pm 0{\cdot}03, \quad \text{♂} = 0{\cdot}82 \pm 0{\cdot}01.$$

Le rapport ♀/♂ calculé de cette façon = 1·5.

On doit cependant se demander si, d'une manière générale, nous sommes en droit d'opérer la conversion des indices de couleur en unités d'hormone à l'aide de la courbe de Tatum et Beadle. En effet, cette courbe a été établie par des injections d'extraits qui diffèrent très sérieusement des implantations en ce qu'elles comportent l'injection, *en une fois*, d'hormone toute faite; tandis que, dans le cas des implantations, il s'agit de *diffusion graduelle, à partir de l'implant, de l'hormone formée au fur et à mesure*. Ces deux processus ne sont pas nécessairement équivalents. Notons, d'autre part, que la courbe de Tatum et Beadle est formée par les valeurs maxima; tandis que nous venons de convertir des moyennes.

Variation de l'effet avec le nombre d'implants

Ainsi notre première tâche est de vérifier si (ou dans quelles conditions) la courbe de Tatum et Beadle est applicable aux effets produits par des implants. Cette vérification peut être faite par l'implantation de nombres différents d'implants et *en supposant* (ce qui nous paraît raisonnable) *qu'il y a stricte proportionnalité entre le nombre d'implants et la quantité d'hormone formée*. La colonne 3 du tableau 2 et la fig. 1*A* donnent les indices moyens trouvés. La colonne 4 du même tableau donne ces valeurs converties en unités d'hormone d'après la courbe de Tatum et Beadle. On voit que les valeurs trouvées ne sont pas proportionnelles aux nombres d'implants. Les courbes pleines de la fig. 1*B* sont les courbes théoriques calculées en supposant que 2, 3 et 4 implants donnent 2, 3 et 4 fois plus d'hormone qu'un seul. On voit que les courbes pointillées, reliant les points expérimentaux, restent constamment en dessous des courbes théoriques.

Lorsqu'on cherche les raisons de ce décalage systématique, on constate d'abord qu'à mesure que

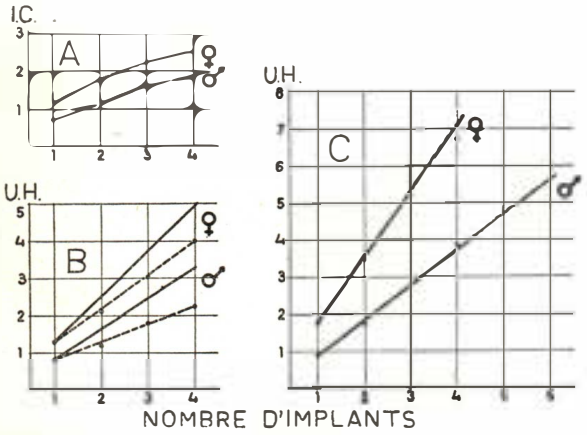

Fig. 1. Effet de 1, 2, 3 et 4 implants *w* ♀ ou ♂ sur des hôtes *v bw* ♂. (*I.C.*, Indice de couleur. *U.H.*, Unités d'hormone.)

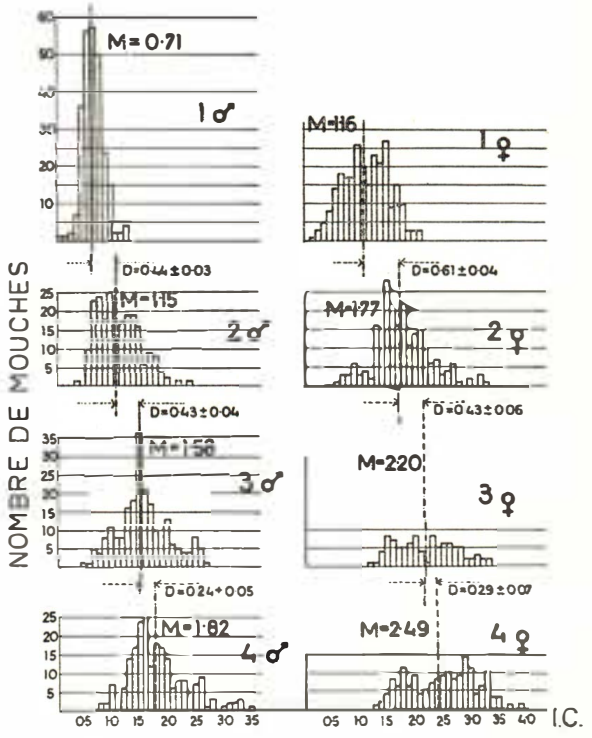

Fig. 2. Effet de 1, 2, 3 et 4 implants *w* ♀ ou ♂ sur des hôtes *v bw* ♂. (*I.C.*, Indice de couleur.)

Tableau 2

Nombre et sexe des implants	*n*	Indice moyen du total	Indice, converti en unités d'hormone: Du total	De la moitié supér.	Du tiers supér.	Du quart supér.
1♂	254	0·71 ± 0·01	0·82	0·86	0·89	0·93
2♂	215	1·15 ± 0·03	1·21	1·46	1·63	1·74
3♂	220	1·58 ± 0·03	1·78	2·29	2·58	2·80
4♂	214	1·82 ± 0·04	2·24	2·99	3·49	3·86
1♀	258	1·16 ± 0·02	1·23	1·51	1·67	1·76
2♀	219	1·77 ± 0·03	2·11	2·78	3·20	3·48
3♀	97	2·20 ± 0·05	3·06	4·26	4·85	5·23
4♀	160	2·49 ± 0·05	4·00	5·61	6·32	6·71

les valeurs absolues des effets montent, la variabilité autour des moyennes devient de plus en plus forte; l'étalement des courbes de distribution augmente (fig. 2), les maxima se déplaçant beaucoup plus que les minima. On est en droit de se demander si ce n'est pas cette variabilité qui cause le décalage de nos courbes par rapport aux courbes théoriques.

Causes de la variabilité des effets

Nous avons donc été amenés à étudier quelques causes possibles de cette variabilité. Il faut signaler ici que, dans toutes nos expériences, l'âge des donneurs, ainsi que celui des hôtes, était connu à 2 heures près; d'autre part nous opérions toujours avec des

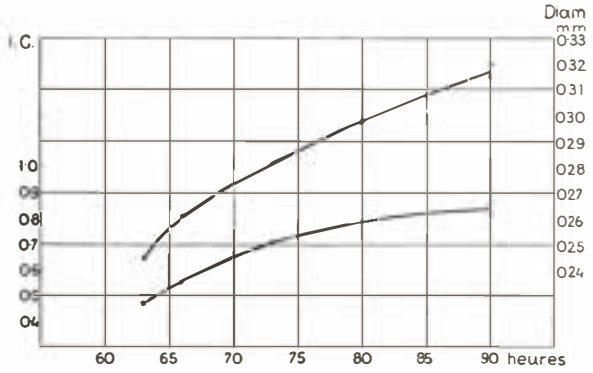

Fig. 3. Relation entre l'âge de l'implants au moment de l'implantation (en heures à partir de l'éclosion de la larve) et l'effet sur l'hôte. La courbe supérieure donne la taille finale de l'implant. (*I.C.*, Indice de couleur.)

animaux d'un même âge. Cependant l'observation montre que tous les implants ne se développent pas également bien.

Nous avons examiné d'abord si l'effet sur les hôtes dépendait de l'âge des implants au moment de l'implantation. Le graphique de la fig. 3 montre que l'effet augmente avec l'âge du donneur. La courbe supérieure montre que la taille finale des implants monte aussi.

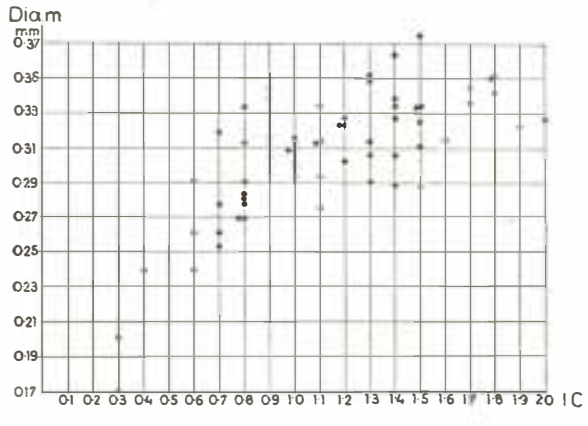

Fig. 4. Corrélation entre le diamètre des implants et l'effet sur l'hôte. (*I.C.*, Indice de couleur.)

Nous avons ensuite fait une statistique de la taille des implants provenant d'hôtes dont l'indice de couleur a été déterminé préalablement. Cette statistique (fig. 4) met en évidence une corrélation très nette entre la taille finale des implants et l'effet sur l'hôte, corrélation particulièrement importante aux basses valeurs des diamètres des implants.

Enfin, nous avons pu nous rendre compte qu'il existe une corrélation entre la position de l'implant

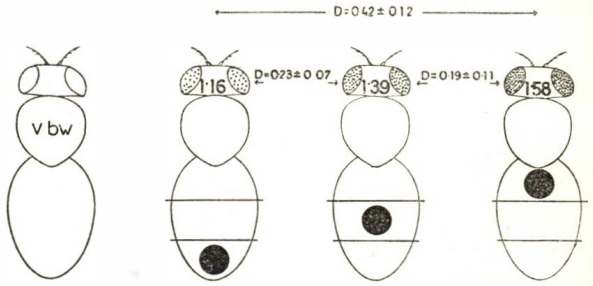

Fig. 5. Corrélation entre la position de l'implant et l'effet sur l'hôte. Les chiffres indiquent l'indice de couleur moyen.

dans l'abdomen de la mouche et l'effet sur celle-ci (fig. 5).

Si, on compare maintenant les résultats des implantations de 1, 2, 3 et 4 implants, on a l'impression que le pourcentage d'implants mal développés croît avec le nombre d'implants (sans qu'il soit facile d'évaluer ce facteur numériquement). De même on comprend que la position moyenne des implants n'est pas la pareille dans ces différents cas.

Méthode des maxima et ses résultats

Toutes ces observations nous ont conduit à la conclusion que les valeurs supérieures trouvées pour chaque lot sont probablement plus significatives que les moyennes ordinaires. Les colonnes 5, 6 et 7 du tableau 2 montrent en effet que les valeurs se rapprochent de plus en plus de la proportionnalité (au nombre d'implants) à mesure qu'on utilise pour le calcul une fraction de plus en plus restreinte des valeurs supérieures; et la courbe *C* de la fig. 1 montre que cette proportionnalité est atteinte lorsqu'on prend *la moyenne du quart supérieur* des valeurs expérimentales.

Il semble donc raisonnable de tenir compte non pas des moyennes ordinaires converties en hormone d'après la courbe de Tatum et Beadle, mais de la moyenne fournie par le quart supérieur des valeurs

expérimentales traduites en hormone. Nous obtenons ainsi pour les ♀♀ et ♂♂ *w* les valeurs suivantes:

♀ = 1·76, ♂ = 0·93, Rapport ♀/♂ = 1·9.

Par ailleurs, l'examen des courbes des maxima pour les ♀♀ et les ♂♂ (fig. 1), montre qu'il y a une bonne correspondance des valeurs trouvées pour

1♀ (1·76 ± 0·03) et 2♂ (1·74 ± 0·05),
2♀ (3·48 ± 0·16) et 4♂ (3·86 ± 0·19).

A elle seule, cette constatation suffit déjà à rendre vraisemblable un rapport; ♀/♂ voisin de 2. Si maintenant on construit un graphique où l'on porte en abscisse l'inverse de la fraction des valeurs utilisée pour le calcul et, en ordonnée, le rapport trouvé pour chacune de ces fractions, on obtient la courbe de la fig. 6 qui montre nettement que ces rapports tendent vers une limite située entre 1·8 et 2·0.

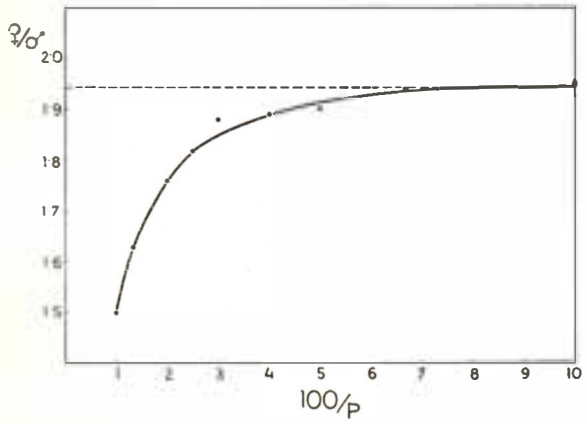

Fig. 6. Rapports entre la production d'hormone v^+ par des implants *w* ♀ et ♂, calculés à partir de pourcentages différents de données expérimentales. (*P*, pourcentage.)

Comparaison avec l'étalonnage d'après la courbe des indices de couleur

Notons maintenant que la courbe des indices de couleur dont nous sommes partis (fig. 1*A*), nous fournit, un moyen direct de determiner la libération relative d'hormone, moyen indépendant de toute conversion en unités d'hormone d'après la courbe de Tatum et Beadle. Les valeurs ainsi obtenues sont exprimées en "*unités* ♂ *w*" si nous nous servons de la courbe d'indices trouvée pour les implants ♂♂. L'indice moyen trouvé pour l'œil ♀ *w* était = 1·16, ce qui sur cette courbe correspond à la libération d'hormone par deux yeux ♂. Le rapport ♀/♂ trouvé de cette manière est donc = 2·0.

On voit que les résultats fournis par les deux méthodes s'accordent d'une manière tout à fait satisfaisante.

Conclusions

En partant de l'hypothèse que la quantité d'hormone formée est proportionnelle au nombre d'implants (hypothèse qui semble vérifiée), nous arrivons donc à la conclusion que lorsque le dosage du gène v^+ passe de 1 à 2, la quantité d'hormone (c'est-à-dire probablement aussi la vitesse de réaction) se trouve multipliée par un coéfficient voisin de 2.

Les expériences que nous poursuivons maintenant sont destinées à montrer si la production d'hormone augmente proportionnellement au dosage lorsqu'on introduit une troisième dose du gène v^+. Les résultats que nous avons obtenus jusqu'ici par deux méthodes différentes—en nous servant de superfemelles, d'une part, et d'une duplication pour *v*, d'autre part—semblent indiquer que la production de l'hormone v^+ augmente encore. Nos statistiques ne sont pas encore suffisantes pour établir la valeur exacte du rapport; les chiffres obtenus jusqu'ici, et que nous ne pouvons donc considérer qu'avec réserve, sembleraient indiquer que l'introduction d'un troisième gène v^+ n'entraîne pas une augmentation proportionnelle de la production d'hormone. Si ces données préliminaires se vérifient, il nous faudra expliquer cette limitation en tenant compte de la proportionnalité de la production d'hormone au nombre d'implants. Une telle situation pourrait trouver son explication, par exemple, dans l'existence, dans les cellules-mêmes de l'implant, d'une réserve limitée de matières premières requises pour la fabrication de l'hormone.

Il y a lieu de signaler à ce propos que Kühn, Caspari et Plagge (1935) ont examiné l'effet du dosage du gène *A* de l'*Ephestia kuhniella* sur la production de l'hormone *A*, par implantation d'ovaires d'animaux homo- ou hétérozygotes. N'ayant pas trouvé de différence entre l'action des ces implants, les auteurs en ont conclu à l'existence d'une "réaction primaire" déclenchée aussi bien dans les deux cas et précédant la formation de l'hormone *A*. Rien, dans nos expériences, ne permet jusqu'ici de mettre en évidence ce chaînon intermédiaire entre le gène v^+ et l'hormone v^+. L'hypothèse d'une réserve limitée de matières premières rendrait compte de l'observation de Kühn, Caspari et Plagge sans fair intervenir une "réaction primaire".

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ERNST, A. ***Heterostylie als Problem der Evolution***

Schaffung gesicherter Grundlagen für die Entwicklungstheorie ist zur Zeit eines der wichtigsten *theoretischen* Ziele der Vererbungs- und Mutationsforschung. In dieser Richtung gehen die vom Vortragenden seit zwei Jahrzehnten durchgeführten Untersuchungen zur genetischen Analyse der *Heterostylie*, einer der mannigfaltigen Variationen in Bau und Funktion der Blüten, deren Bedeutung darin gesehen wird, dass sie die *Fremd*bestäubung fördern und *Selbst*bestäubungen ausschliessen oder unwirksam machen.

Der Blütendimorphismus äussert sich bei den heterostylen Primeln, dem Untersuchungsobjekt des Vortragenden, in der Ausbildung von *Lang*griffelblüten, in denen die Narbe die tiefer stehenden Antheren überragt, und von *Kurz*griffelblüten, deren Antheren *über* der tiefsitzenden Narbe stehen. Bestäubungen zwischen Organen gleicher Höhenlage sind *legitim*; sie haben volle Fertilität zur Folge, während nach allgemeiner Annahme Bestäubungen zwischen Organen in verschiedener Höhenlage der Blüten *illegitim* sind, einen verminderten Fertilitätsgrad aufweisen, oder ganz ergebnislos bleiben.

Ausser diesen beiden allbekannten Haupttypen ist für einzelne Primeln, Ch. Darwin hat schon 1877 darüber berichtet, *Homostylie*, Ausbildung von Blüten mit Narbe und Staubbeuteln in gleicher Höhenlage, bekannt.

Morphologische, physiologische und genetische Studien an homostylen Formen der Gartenaurikel und der alpinen Wildart *Pr. viscosa* haben zum Ergebnis geführt, dass die "normalen" Lang- und Kurzgriffel nur zwei von acht möglichen Kombinationen je zwei verschiedener Griffellängen, Antherenstellungen und Pollenkorngrössen sind. Von diesen acht Kombinationen sind drei bei der Kulturform *Pr. hortensis*, deren sechs bei der Wildart *Pr. viscosa* gefunden und genetisch analysiert worden.

Die Formulierung des Erbganges der Heterostyliemerkmale ist in dem untersuchten Formenkreis ebensowohl auf Grund der Annahme *sehr starker Koppelung* besonderer Gene für Lang- und Kurzgriffligkeit, hohe und tiefe Antherenstellung, grosse und kleine Pollenkörner oder von *multipler Allelie mit pleiotropem Effekt* möglich. Dem letzteren Erklärungsversuch wird der Vorzug gegeben und für die normal dimorphen Primeln eine *selbstfertile monomorphe Stammform mit langem Griffel, hochstehenden Antheren und grossem Pollen angenommen*. Von dieser Stammform ausgehend ist die Entstehung eines Schwarmes *mutierter* Formen, Kleinarten inbezug auf die Merkmale der Blütenplastik, denkbar. In diesem Formenschwarm sind mit den morphologischen auch physiologische Unterschiede, i.b. in den *Fertilitäts*- und *Vitalitäts*verhältnissen, kombiniert. Kurzgrifflig gewordene Mutanten z.B. sind nicht mehr fertil für den Pollen der Stammform, während Mutanten mit kleinem Pollen die langgrifflige Stammform und langgrifflig gebliebene Mutanten nicht mehr zu voller Fertilität zu bringen vermögen. Dagegen erweisen sich die Mutanten mit veränderter Griffellänge, veränderter Antherenstellung und Pollengrösse untereinander reziprok fertil. Von den mutativ entstandenen acht Allelen des Gens für die Blütenplastik sind die *partiell* rezessiven Typen für *Kreuz*bestäubungen ungünstig und bei der Mehrzahl der jetzt dimorphen Arten ganz oder fast ganz ausgemerzt worden. Nur die beiden extremen Allele, welche entweder Dominanz oder Rezessivität in allen Merkmalen des Heterostyliekomplexes übertragen, sind erhalten geblieben.

Ob die an den natürlichen Standorten der untersuchten Wildart *Pr. viscosa* zu *ca.* 1·5 % auftretenden abweichenden Phäno- und Genotypen als letzte Reste des während des Ueberganges vom Mono- und Dimorphismus der Blüten entstandenen primären Formenschwarmes oder als Rückmutationen neuern Datums zu deuten sind, musste dahingestellt bleiben. Die Ausdehnung der Untersuchungen auf *asiatische* Primeln hat seither gezeigt, dass der erstern Deutung ein höherer Wahrscheinlichkeitsgrad zukommt.

Homostyle Typen asiatischer dimorpher *Primula*-Arten kommen nicht nur in den Zuchten der Gärtner und Genetiker vor, wie z.B. bei *Pr. sinensis*, *kewensis*, *malacoides*, *cortusoides*, sondern sind für diese und andere Arten durch Herbarstudien auch in den Populationen der natürlichen Standorte festgestellt worden. Des weitern haben die Untersuchungen, die der Vortragende seit drei Jahren unter Benutzung der reichen, einzig dastehenden Primula-Kollektionen des Botanischen Gartens in Edinburgh and seines Primula-Herbariums durchgeführt hat, zu dem überraschenden Resultat geführt, dass in der Gattung *Primula* neben dimorphen auch eine beträchtliche Zahl *monomorpher Arten* vorkommen. Diese entsprechen in ihrer Blütenplastik durchaus der auf Grund der Untersuchungen an den europäischen Primeln aufgestellten hypothetischen Stammform: sie haben lange Griffel, hochstehende Antheren, grossen Pollen und sind bei spontaner und künstlicher Selbstbestäubung absolut fertil.

Zwischen monomorphen und dimorphen Arten der Primula-Sektion Candelabra sind zahlreiche Kreuzungen gelungen. Die Analyse dieser Nachkommenschaften, das vergleichende Studium der Mutabilität der durch Kreuzungen erhaltenen homozygoten Homostylen europäischer Aurikeln und monomorpher asiatischer Arten werden weitere Aufschlüsse zur angestrebten genetischen Analyse der

Heterostylie ergeben und darüber hinaus eine vielversprechende Grundlage schaffen, für die Bestimmung der Wirkungsweise von *Selektion* und *Isolierung* im Evolutionsprozess, der vom Monozum Dimorphismus der Blüten führt.

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Ernst, A. ***Vererbung teratologischer Merkmale durch labile Gene***

Die Mehrzahl aller Merkmale von Blütenpflanzen, für welche bis jetzt Vererbung durch *mutable*, *unstabile* oder *labile* Gene angegeben worden ist, bedeuten *Abweichungen von einer Norm.* Sie fallen in der Regel derart auf, dass sie im morphologischen Sinne als Anomalien, Missbildungen beschrieben worden sind.

Die bekanntesten dieser bei Blütenpflanzen als *Mutationen* nachgewiesenen Anomalien bestehen in Abänderungen der Farbe von Laub- oder Blütenblättern, Veränderungen in der Form von Laub- oder Blütenblättern oder in Form und Wuchsart ganzer Sprosse. Besonders häufig machen sich Anomalien, die auf *labilen* Genen beruhen, in der Blütenregion geltend. Sie können in Änderungen der Symmetrie- und der Zahlenverhältnisse in den einzelnen Blattkreisen, in der Ausbildungsart der Blumenkrone, aber auch des Kelches, der Staub- und Fruchtblätter, beruhen. Besonders auffällig sind die verschiedenen Möglichkeiten der *Blütenfüllung*: die Petalodie, mit Umwandlung von Staubblättern in Kronblätter, die Petalomanie, d.h. Vermehrung der Kronblattzahl durch Teilung der Kronblattanlagen, die Sepalodie, d.h. die kelchartige Ausbildung der Blumenkrone und schliesslich die in umgekehrter Richtung gehende Calycanthemie, die Ausbildung einer zweiten Blumenkrone durch Umwandlung des Kelches.

Der Vortragende bespricht die Vererbung der *Calycanthemie* bei Primeln. Sie bietet, verglichen mit andern pflanzlichen und tierischen Objekten, an denen Erbgange durch labile Gene studiert worden sind, mehr für Verständnis und Auswertung der Resultate bemerkenswerte Vorteile. Sie dürfte zur Zeit vielleicht die eingehendste Analyse des Erbganges einer Bildungsanomalie sein.

Die in Form von Stammbäumen wiedergegebenen Resultate der Analyse einer Nachkommenschaft von *ca.* 50 000 Individuen in fünf Generationen, die auf *eine* Stammpflanze zurückgehen, haben gezeigt, dass mutative Abänderungen des Gens für Calycanthemie überall, in somatischen und generativen Organen und Geweben erfolgen können. Sie sind nicht in allen Individuen derselben Sippe und lange nicht in allen Sippen gleich häufig. Aus den Resultaten von Kreuzungen zwischen calycanthemen Gartenformen und normalkelchigen Weilformen geht z.B. hervor, dass das *genotypische Milieu*, der Einfluss anderer Gene desselben Genoms und *plasmatische Einflüsse*, die Nachkommenschaften in starkem Grade selektiv hinsichtlich Penetranz und Expressivität des Calycanthemiemerkmals beeinflussen.

Die Untersuchungen über den Erbgang der Calycanthemie haben sodann auch den Nachweis dafür erbracht, dass eine erbliche Anomalie, die auf einem labilen Gen beruht, durch Kombinationskreuzungen nicht nur Stärkung, sondern auch *Schwächung* ihrer Penetranz und Expressivität erfahren kann, die relativ häufig und rasch, unter völliger Ausmerzung der Anomalie, dauernd zum Normalzustand zurückführt. Diese Feststellung dürft nicht nur für das Verständnis des Erbgeschehens im Pflanzen- und Tierreich, sondern auch für eines der wichtigsten Gebiete der menschlichnen Erblichkeitsforschung, die Vererbung von Missbildungen und Erbkrankheiten, bedeutungsvoll sein. Wenn bei Pflanzen gerade Bildungsabweichungen und Missbildungen besonders häufig durch labile, leicht mutierende und völlig zum Gen der Norm zurückschlagende Gene vererbt werden, stellt sich die Frage zur Diskussion, ob nicht auch unter den Bildungsabweichungen und Erbkrankheiten des Menschen solche vorhanden sind, die nicht auf *stabilen*, sondern auf *labilen* Genen beruhen, für welche also unter gewissen Umständen ebenfalls eine Abschwächung resp. Ausmerzung in befallenen Sippen zu erwarten ist.

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Eyster, W.H. ***Genetic Study in the Genus*** **Tagetes**

All of the named species of *Tagetes* appear to be indigenous to the Western Hemisphere and are limited to Central America and Mexico with the exception of a few species which extend as far south as Chile and as far north as southern United States. Recently in central Tibet a variety of *Tagetes* was collected which appears to be a species of *T. erecta.* Of the more than thirty species, *T. erecta* and *T. patula* have been grown for centuries in many of the civilized countries of the world as ornamental plants.

T. erecta includes a large number of horticultural varieties which are commonly known as African marigolds. These horticultural varieties represent various combinations of genetic variations in length of stem, colour and structural characteristics of the leaves, number and distribution of the oil glands, type of branching, size and colour of florets, relative numbers of ray florets and disk florets, size and shape of the flower heads, time of flowering, and colour of the mature achenes. Genetic types with a single cycle of ray florets are called "single heads", while those

that have many cycles of such florets are called "double heads". The ray florets are invariably male sterile and the disk florets are hermaphroditic. Genetic strains in which the heads are made up exclusively of ray florets are entirely male sterile and are valuable for the production of commercially important hybrids. Other strains have heads made up entirely of disk florets. Flower colours range from light primrose to very deep orange, with the lighter colours recessive to the deeper ones.

The variety of *T. erecta* collected in Tibet lacks entirely or has only vestigial oil glands incapable of secreting the odoriferous oil. This odourless character is inherited as a recessive. A genetic strain having rudimentary functionless oil glands was found in Guinea Gold, a horticultural variety of *T. erecta*. These rudimentary glands likewise are inherited as a recessive character. Glandless plants × rudimentary glanded plants gave rise to normal gland-bearing plants in the F_1, and normal gland-bearing and odourless plants in the ratio of 9:7 in the F_2 generation.

T. patula likewise includes a large number of horticultural varieties which represent various combinations of genetic variations. Although the species is smaller in all respects as compared with *T. erecta*, the varieties are quite similar to those of the latter species except that the flowers may contain anthocyanin. The flowers have plastid pigments ranging from light primrose to deep orange with or without the anthocyanin pigments. The anthocyanin may occur in almost imperceptible amounts, in amounts that render the flowers deep red, or in varying intermediate amounts.

T. erecta is a 24-chromosome species, *T. patula* a 48-chromosome species, while their interspecific hybrids have 36 chromosomes. These chromosome differences are expressed in the different sizes in the stomata and the pollen grains. The interspecific hybrid has a sterility of about 98·75 %.

Weak aqueous solutions of colchicine induce chromosome doubling in these species of *Tagetes* as well as in their hybrids. By immersing the tips of 8–10 in. plants in a colchicine solution the growing tip is killed, but axillary shoots are formed of which a relatively high percentage have an increased number of chromosomes.

83

FABERGÉ, A.C. ***An Experiment on Chromosome Fragmentation by X-rays in*** **Tradescantia**

X-ray treatment was administered during the resting stage in immature pollen of *Tradescantia bracteata*, and the resulting chromosome fragments were counted in the microspore division metaphases 70 hr. after treatment. A comprehensive experiment with twelve treatments was made as follows: Three dosages of 1320, 2640 and 3960 r. units were given each dosage either continuously in 18 min. or in 3 min. runs during 3 hr. (a ten-fold fractionation), each combination of dosage and fractionation being given with the material kept at 15 and at 30° C. The experiment is replicated so as to give a valid estimate of error; 1080 cells were scored, and over 10,000 chromosome pieces counted.

Within the fiducial limits of the experiment it can be said that:

(1) The effect of increasing dosage is linear.

(2) Fractionation diminishes the number of fragments, more so at higher dosage.

(3) Higher temperature diminishes the number of fragments, more so at higher dosage.

(4) Fractionation acts alike at both temperatures.

(5) There is no triple interaction between dosage, fractionation and temperature.

The reduction in the number of chromosome pieces by fractionation of dosage means that a repair process exists. It is not inconsistent with the data that breaks are initially produced by a "direct" action, as are lethals in *Drosophila*, though the conclusion seems inescapable that *Tradescantia* chromosomes differ in some respects from those of the former organism.

If the view is accepted that breaks are induced "directly", then the repair process in its entirety must be identified with chromosome rejoining. No detailed physical theory of the rejoining process is at present possible. Nevertheless, the present data define the conditions which any such theory must satisfy in a fairly stringent and specific manner. Even with the simplest possible assumptions, the repair process must be very complicated. The so-called "contact hypothesis" is very difficult to reconcile with the data.

It is very likely that a considerable proportion of the "repairs" are reconstructions of the old linear sequence, and they are not detectable cytologically.

It is emphasized that replication is absolutely necessary in work of this kind. Variation between buds treated alike is much greater than that between cells in the same bud, and an experimental error derived from the latter is quite inadequate.

84

FANKHAUSER, G. ***Polyploidy in Salamanders***

Because of the comparative scarcity of polyploidy among animals, the natural occurrence of triploid embryos in Amphibia, first discovered by G. and P. Hertwig and by Dalcq, deserves special attention. In the American newt, *Triturus viridescens*, these exceptional triploid individuals may be identified in an early larval stage by chromosome counts in ampu-

tated tail-tips, and followed through larval development and metamorphosis.

The tail-tip preparations also demonstrate that the triploid nuclei and cells are generally larger than the diploid. The examination of serial sections through animals preserved after metamorphosis shows that the proportionality between chromosome number, nuclear and cell size obtains in all organs and tissues studied so far. However, organ size and body size of triploid animals are not usually increased. This absence of gigantism is due to a reduction in cell number in the various organs which compensates for the increase in size of the individual cells. A possible exception was found in the case of the notochord which appears to have, in cross-sections, about the same number of cells in triploid and diploid animals, and is therefore larger in the triploid. Aside from this, cell number is not constant for the species but controlled by a regulating factor which keeps organ and body size within, or close to, normal limits.

The validity of this conclusion was confirmed by more recent observations on larvae of a lungless salamander, *Eurycea bislineata*, where triploidy seems to be much more frequent (thirteen of the 134 larvae examined so far) and where tetraploidy also occurs, though much less frequently (two of 134 larvae). In diploid, triploid and tetraploid larvae, there is close proportionality between chromosome number, nuclear and cell size. In the living larvae, this is indicated by the size and spacing of the pigment cells on head and body.

Gigantism is conspicuously absent among polyploid larvae of *Eurycea*. While some of the triploid larvae may show a slight increase in body size, the two tetraploid larvae are actually smaller than the controls and slightly less vigorous. This may indicate that any further increase in chromosome number may be incompatible with normal development. Since tetraploid cells are about twice as large as diploid cells, the cell number in the various organs and tissues of tetraploid larvae is probably reduced to about one-half the normal value. We may expect that, in a vertebrate, an increase of the size of the individual cells to twice the normal volume, coupled with a reduction of the cell number by 50%, will have important physiological consequences.

In addition to the quantitative effects caused by the increase in chromosome number, triploidy, as might be expected, also causes disturbances of the normal process of sex differentiation. The investigation of the effects of triploidy on sex, which is under way, is greatly facilitated by the high frequency of natural triploidy in *E. bislineata*, and by the recent discovery that triploidy may be induced in the newt by cold treatment of eggs at the beginning of development.

85

FELDMAN, W.M. ***The Inheritance of Congenital Transposition of the Viscera***

Notwithstanding the genetic relationship between the partial and complete varieties of visceral transposition, this paper deals only with the complete variety. Strictly speaking, transposition is never quite complete, because not only are the cerebral centres not transposed—the incidence of left-handedness is no greater in people with this condition than in the general population—but the great vessels of the heart are, as far as I know, in their proper positions.

The condition was first discovered in man in the sixteenth century, during dissection of the bodies of criminals. When, in the course of routine clinical and radiological examinations, it was discovered that the condition tended to occur in more than one member of a family, an hereditary basis was suspected. That it is not a dominant character follows from its great rarity (about 1:15,000), and from the fact that it occurs more often in members of the same sibship than in those of successive generations of the same family. E. A. Cockayne first suspected the condition to be a Mendelian recessive, and analysis of all the recorded cases, especially those recorded and investigated by myself, proves his surmise to be correct. Analysis shows that:

(1) The condition occurs most frequently in children of parents each of whom is normal (= heterozygous).

(2) Several members of such a sibship may have the same abnormality.

(3) The ratio of normal to abnormal children in all the 119 sibships (539 children) collated by Cockayne approaches the theoretical 3:1.

(4) The incidence of parental consanguinity is uncommonly high in such cases—11% among the fifty-three sibships analysed by Cockayne as against the less than 1% in the general population. In one family investigated by myself, the two normal parents were first cousins, and of the twelve children born to them, five were subjected to clinical and X-ray examination, out of whom three showed the abnormality.

(5) The condition is sometimes found in parent and child. The normal parent in such cases must be presumed to be heterozygous. It has also been recorded in grandparent and grandchild, in uncle and nephew, as well as in cousins, but children of an abnormal parent are normal.

(6) If one member of a pair of monozygotic twins shows the condition it is generally found also in the other member of the pair.

These facts point to the character being a Mendelian recessive. There is no record yet of a case in which all the children of two abnormal parents were found to

possess the abnormality. There is, however, the disturbing fact that in five cases of monozygotic twins the abnormality was present in only one member. The discrepancy is too great to be accounted for on the supposition that in those cases both co-twins were originally heterozygous, but that either the whole chromosome carrying the dominant gene was lost, or a mutation occurred in its gene, in the daughter cell from which the twin with the transposed viscera arose. Similar difficulties have arisen in connexion with other genetic problems. Cases of conjoined twins, for instance, have been recorded in which not only was such an abnormality as harelip and cleft palate present in only one of the components, but even where the sexes, as judged from the external genital organs, were typically male and female respectively. I know of at least two such cases. In one pair of pygopagi that came under the observation of Dr Szendi of Debrecen, Hungary, the internal genital organs of the apparent male were, it is true, found to be female, but as hermaphroditism is genetically akin to hypospadias, which is an hereditary character, such a finding is equally difficult to explain. Moreover, visceral transposition has sometimes been found in one only of the components of conjoined horns (never in both).

Linkage of the character of visceral transposition with other pathological characters (congenital morbus cordis, absence of organs, duplication of organs, bronchiectasis, etc.) is discussed.

86

Ferriman, D. ***The Genetics of True Oxycephaly and Acrocephalosyndactyly***

The paper is based on personal observations and literature records. Dr Penrose has kindly interpreted the data. The author believes that cranio-facial dysostosis and oxycephaly are one and the same disease. Acrocephalosyndactyly shows the same skull changes as oxycephaly, with the addition of changes in the hands and elsewhere. Both oxycephaly and acrocephalosyndactyly are due to hereditary defects of the germplasm. Records of 188 families containing oxycephalics were found in literature. Of these, twenty-three clearly and twenty-one others less certainly, gave evidence of heredity. The author investigated five families, of which two unquestionably and one possibly, showed heredity. Seventy families containing cases of acrocephalosyndactyly were found in literature, of which four were undoubted examples of inheritance, ten possibly so. Both diseases are inherited in a dominant manner. The evidence for oxycephaly is as follows. Two generations are clearly involved in eight families from literature, and in one of the author's. Three generations are probably involved in five families, and four in another, though in none are the facts established beyond dispute for more than two generations. One of the author's families is believed to be the first in which the facts are established with certainty in three generations. The incidence of third cousin marriages is no greater than in the population at large, being recorded only twice in the whole series. Of acrocephalosyndactyly families, three are clearly involved through two generations. First cousin marriages are described only once. There is evidence for the existence of modifying genes. Fuss and Waardenburg, who examined their families in detail, emphasize the existence of extremely mild cases. In one of the author's families the grandfather and one of his granddaughters are grossly affected, whereas in the granddaughter's mother the oxycephalic features are only dimly discernible.

Three hypotheses may be advanced to account for the relationship of oxycephaly and acrocephalosyndactyly. The first is that two independent genes are at work, one causing oxycephaly, the other syndactyly. The second, that a single gene responsible for the whole syndrome may be so modified in certain cases that syndactyly is suppressed. The third suggests two allelomorphic genes. Only one family clearly shows oxycephaly in one member and acrocephalosyndactyly in another. Dr Penrose is of the opinion that this rules out the first hypothesis, and strongly favours the third. A marked difference in sex incidence supports this view. The association of acholuric jaundice and oxycephaly may be due to a third allelomorph. The proportion of sporadic to familial cases, high in oxycephaly and higher still in acrocephalosyndactyly, is probably a consequence of the lethal effect of this disease.

87

Finney, D.J. ***An Apparent Linkage of the OAB Blood Groups with Allergic Disease***

Methods of analysis of pedigrees covering two generations for purposes of linkage detection, which were originated by R. A. Fisher, have been extended by the present author during research work at the Galton Laboratory. Each family is assigned a score, the composition of which is determined by the parental phenotypes, whose variance is obtainable from tables. The scores being additive, and their expected values in the absence of linkage being known, a test of significance of the deviation of the total from expectation may be made. If significance is attained, an estimate of the recombination percentage can be made from the score.

This technique was applied to sixty-six families

recorded by Zieve, Wiener and Fries (1936) as having at least one allergic individual. According to these authors, allergy is explicable by a single pair of allelomorphic genes, such that only the recessive homozygotes manifest symptoms prior to puberty. Only twenty-six of the families provided utilizable information for linkage detection, and the deviation of their total score from expectation corresponded to a probability level of 3·9 %. It would thus appear that the data provide strong evidence for the existence of a linkage, an estimate of the recombination percentage being 22·8 %.

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88

FLECKINGER, J. ***Caractères morphologiques et végétatifs en relation avec la triploïdie chez le Pommier et le Poirier***

Les pommiers cultivés sont hétérozygotes; la fécondation est croisée. En outre, ils appartiennent aux deux groupes caryologiques, diploïde et triploïde.

Les variétés, très nombreuses, sont propagées et maintenues par greffage. Selon les exigences culturales, elles sont placées sur franc, sur doucin ou sur paradis.

Pour le poirier, les observations ont porté sur des arbres greffés sur cognassier, en forme de palmettes à quatre branches, disposés en contre-espalier. L'influence du porte-greffe, souvent très variable, en particulier pour ce qui est de la vigueur, n'arrive pas à masquer la très grande vigueur propre aux variétés triploïdes de pommiers et de poiriers, qui se font remarquer, par l'ample développement de l'arbre. L'allongement des rameaux est plus fort et la surface et l'épaisseur des feuilles sont généralement très grandes.

Chez le poirier, l'échelle de variation d'épaisseur du limbe varie pour l'ensemble des variétés diploïdes de 19 à 27 dixièmes de mm. pour 10 feuilles, avec une plus grande fréquence pour 22. Elle varie de 29 à 32 pour les variétés triploïdes, la plus grande fréquence paraissant être vers 30 à 31.

La surface des feuilles varie de 50 à 75 cm.^{2} chez l'ensemble des variétés triploïdes, et de 15 à 45 cm.^{2} chez l'ensemble des variétés diploïdes. Chez le pommier, la variation d'épaisseur des feuilles est de 20 à 25 dixièmes de mm. pour les diploïdes et de 28 à 35 dixième de mm. pour les triploïdes, la plus grande fréquence étant de 23 pour les diploïdes, et de 31 à 32 pour les triploïdes.

Ce grandissement systématique de tout ce qui est measurable, laisse soupçonner le développement naturel important que prendraient les arbres originaux des variétés triploïdes sur leurs propres racines, et donne à penser que le type tétraploïde de pommier, découvert par Johanson en 1937, dans la descendance d'hybride de triploïde par diploïde, doit mener à un véritable gigantisme.

Enfin, une constatation générale s'impose: l'étroit parallélisme entre les espèces Pommier et Poirier.

89

FORD, E.B. ***The Genetics of Growth and Differentiation***

The growth of an organism as a whole, and of its parts, is under genetic and environmental control. Genetically it may be determined by the most diverse means, operating physiologically in a great variety of ways. Thus the total size of an organism may be under the major control of a single factor pair. On the other hand, very numerous genes, approximately equal in effect, may co-operate to determine it. On the physiological side, the genetic or cytological situation may influence cell size (tetraploids are normally larger than diploids), or cell division, more or less directly. However, its effect on growth may be of a more indirect kind. For example, genes controlling the development of the ductless glands will modify total body size in mammals. Thus a type of recessive dwarfing in mice is due to a single factor pair which affects the development of the anterior pituitary.

It is known that the size of the parts of the body usually bears a simple relation to that of the whole. If y be the size of an organ and x the size of the body minus that organ, then $y = bx^{\alpha}$, where b and α are constants. Both b, determining the initial relationship (the value of y when $x = 1$) and α may be under simple (or more complex) genetic control. Thus genes affecting absolute body size may bring about changes in *proportion*, themselves genetically determined.

Not only growth rates but other developmental processes may be under simple genetic control. Thus it has been shown in *Gammarus*, and in a variety of other organisms, that genes may determine the rate at which processes (e.g. pigment deposition) can take place in the body, and the time at which they begin.

In considering growth and differentiation, it is especially important to bear in mind that any organism represents genetically a highly organized system. The genes are accurately balanced against one another, for they interact to produce the characters for which they are responsible and give rise to multiple effects. Thus any alteration in one or more pairs of allelomorphs may modify the *effects* which other genes produce.

Heterosis, or hybrid vigour, leading to increased size in the offspring of a wide cross, is due principally to the masking of recessives by dominants brought in by the opposite parent. But extreme excess (or a reduction) in hybrid size is usually due to ill-adjustment of the gene complex. So too with differentiation: in the fish *Platypoecilus* a sex-linked factor produces dominant black-spotting. In the hybrid between this and another form (*Xiphophorus*), it evokes a fatal cancerous growth. Like all others, genes controlling size and differentiation form part of a highly adjusted system which has been regulated by selection to produce harmonious effects. Changes within it may alter in an unpredictable way the action of genetic units themselves unaffected by the change.

90

FRANKEL, O.H. ***Some Reflexions on Breeding Wheat for Baking Quality***

Breeding for quality is in progress on a large number of agricultural and horticultural plants. More effort has been spent on improving the quality of the wheat grain than that of any other plant product. Methodological and genetical conclusions arrived at may therefore be of interest to everyone breeding for plant quality.

TESTING WHEAT FOR BAKING QUALITY

The success of any breeding scheme depends largely on the significance and reliability of the methods for determining major and minor differences among breeding units. Three main methods of approach are possible in testing for quality: (1) Direct, (2) Indirect, (3) Analytical.

(1) *Direct tests* imitate the economic manufacturing process. The characteristics of a symbol, at least of the finished product—in the case of wheat, a loaf of bread—are used as the standard of value. The methods range from large commercial trials to micro-baking tests. The principles underlying recent methods of test baking are discussed and also the nature of the information which can be gleaned from them.

(2) *Indirect tests* are designed to estimate baking value more rapidly, cheaply, on less material and avoiding "the personal factor". Most methods aim at estimating "baking strength", alleged to depend on gluten quantity and quality. Commonest are the wholemeal fermentation test, gluten swelling test, Extensimeter, Farinograph. Variations, including micro-tests, are available. Crude protein and gluten determinations are also used.

Any tests for the early stages must exclude the possibility of discarding good material. This, however, is shown to exist in most of the above-mentioned tests.

It is questioned whether the need for a test in F_2 and F_3 is as urgent and as general as has frequently been suggested. This is enlarged upon in the discussion on various breeding programmes. Definition in any of these tests is not sufficient in either the high- or low-quality range. By them wheats such as Yeoman might have been discarded. Too great a concentration on quality at this stage might lead to loss of agronomic advances.

Since quality is reported recessive in many crosses, an agronomically promising F_3 family segregating for quality is more valuable than the F_2, but could never arise after rigid quality selection in F_2.

Small-scale tests are, however, valuable for testing selections from "hybrid bulks" and in establishing homozygosity in new varieties.

The question of costs of breeding and testing should not be over-emphasized. Within limits organization should be adapted to the best methods and not vice versa.

Pelshenke's suggestion for a combination of tests is accepted, but such tests should be those whose significance is truly understood and not merely empirical ones.

(3) *Analytical tests* attempt to approach baking behaviour in terms of physical constants and chemical constituents. Schofield, Scott-Blair and Halton have shown that relative strength of flours can be satisfactorily expressed by a relationship between the viscosity and the elasticity modulus of doughs prepared under certain conditions. This work, though directed towards discovering the fundamental physical properties required in a good flour dough, will probably lead to instruments suitable for routine testing. Hullett, in New Zealand, has constructed an instrument which promises to serve for micro-tests.

Brabender independently designed an instrument —the Extensograph—with which the principles discovered in the above work could be applied.

Ultimately all dough phenomena must be referred to their chemical bases. The physical methods referred to above afford the accuracy of description required for the chemical approach, such as the work of Jorgensen and others on proteolytic activity and of McKellar and co-workers on the fractionation of gluten.

This review of the testing problem suggests the conclusion that empirical tests are limited in their significance and reliability, and that only an increased knowledge of the fundamentals can afford a truly scientific approach. It should be admitted that the plant breeder, with his insistence on empirical tests where fundamental knowledge was lacking, all too often has side-tracked the cereal chemist from the

narrow path of scientific approach. It is questionable whether this has been to the ultimate advantage of wheat breeding.

THE INHERITANCE OF BAKING QUALITY

The significance of studies on the inheritance of quality is limited by that of the method of its determination. A number of authors—starting with Biffen (1908)—used kernel structure or nitrogen content. More recently, fermentation time, micro-swelling and micro-extensimeter tests were applied. Many authors state that high quality is recessive and based on a number of polymerous factors. The author, using the fermentation time test, found a prevalence of high-quality F_3 families in crosses Jumbuck (high quality) × Tuscan (low quality), and Reward × Tuscan. Worzella suggested three dominant factors for quality in one cross. As is to be expected in a character of the extreme complexity of baking quality, inheritance studies yield indeterminate and contradictory results. They are applicable only to the material studied and do not permit of general conclusions. It is probable that only with the aid of a truly analytical approach will a genetic approach become possible and valuable.

91

FRENCH, M.H. ***Cattle Breeding in Tanganyika Territory and Some Development Problems Encountered***

Improvement of indigenous zebus by selection and mating of outstanding individuals can only be sucessful if the environment is first improved (e.g. nutrition, management and greater freedom from drought and parasites).

Certain zebus are genetically capable of greater productivity than that finding expression under existing conditions. The progeny of dwarfed cattle that have been stunted over many generations grow into better animals than their parents if removed at birth to good conditions.

Grading up of zebus to European breeds has produced animals much improved in size and productivity in the first cross. This improvement is not maintained by subsequent upward crossing. Higher grades break down constitutionally and are disappointing in their rates of growth, body development and milk yields.

Ayrshire grades break down at a lower level of grading than Friesian.

The constitutional failures are due to factors other than nutrition, though poor feeding accentuates the breakdown.

Linear development is retarded less than live weight, and retardation commences between 6 and 12 months of age.

Long hair accompanies retardation of growth but is not the cause, although it embarrasses the animal.

The temperature-regulating mechanism is impaired and results in slightly higher body temperatures, increased respiratory and metabolic rates. This effect increases with higher grading.

Grade stock digest their food as efficiently as zebus but possibly cannot utilize the digestible nutrients so well, or else have higher maintenance requirements.

The anaemia following piroplasmosis and anaplasmosis is suggested as another inimical factor.

A serious developmental problem exists in grade European stock, the causes of which are not clear.

92

FRETS, G.P. ***Families with Feeblemindedness***

Investigations into the heredity of feeblemindedness have gradually become more extensive.

They were, at first, merely statistical, and later genealogical-statistical, and at the present time the need is felt to make them biographical.

We have now at our disposal many statistical data: putting these in the foreground, we turn to the single families and endeavour to know them as thoroughly as possible, our interest being in families in which feebleminded persons occur, and whether any differences are found among them.

This is the starting-point for my investigations into the heredity and fertility of feeblemindedness.

I do not attempt in the first place to collect a great number of cases, but I examine them very profoundly.

I shall begin with imbeciles who were admitted to our psychiatric institution in 1909. Such patients were then about 20 years old and those still alive are now 50 years of age.

The brothers and sisters have thus, generally speaking, complete families, and still further information can also be obtained from the parents and their brothers, sisters and descendants.

As a first contribution to these investigations, I am investigating five families, starting with persons who were patients in our institution; then five more families will be investigated, the original persons having been so-called "class" patients, coming from a higher social milieu—and in the third place a further five families will be investigated, the original persons having been patients at the Municipal Hospital, who suffered from some bodily sickness or other; this latter material is intended as a control. These are extensive families, the first comprising about 900 persons.

93

FRIEDENREICH, V. *Genetical Problems in Recent Research in Blood Groups*

Highly sensitive serological methods enable us to observe that certain substances (probably carbohydrates) found in almost all body cells and fluids, are not alike in all the individuals of one species. By these differences a species is divided into various serological types. The classical example of this is the division of the human species into types *A*, *B*, *AB* and *O* (Landsteiner's four blood groups). These three characters depend upon allelomorphic genes.

Character "*A*" comprises at least three varieties, differing chiefly quantitatively ($A_1A_2A_3$) and depending upon three different allelomorphic genes. A_1 is dominant to A_2, etc. Recent statistical analyses of the frequency of A_1 and A_2 have given further support to this hypothesis. A_3 is very rare. Its inheritance is demonstrated by some pedigrees.

Successful attempts to distinguish the genotypes *AA* and *AO* serologically have been reported (Dahr). The dominance of the *A* and *B* genes over *O* is not complete. Some theories (Matta, Hirszfeld) based upon these findings are discussed.

The distribution of the group characters in the organism depends upon another gene system (S–s). The gene S acts as a complementary gene and conditions the presence of the respective characters in the tissue cells and secretions. Of animals, only the anthropoids contain true *A* and *B* in their blood corpuscles; soluble *A* and *B* substances, however, occur in many animals. Thus, the value of the group characters as regards phylogenetical considerations seems to be rather limited.

Several observations indicate that human corpuscles contain a great many other serological "factors".

As yet only characters *M* and *N* give rise to really sharp serological reactions. The *MN* system is, genetically, still simpler than the *ABO* system.

The frequency of *N* seems to be very low in Indians and Eskimos. Cases of rare varieties of these characters have been reported. One of these (N_2) seems to depend upon a particular allelomorphic gene.

The existence of "exceptions" from the genetical rules of the *ABO* and the *MN* systems are discussed from a biological and from a medico-legal point of view.

94

GARTH, T.R. *A Review of Race Psychology*

Race psychology has grown from a topic of mere passing interest to a subject of great importance to all people to-day. It has a tremendous bearing on national and international problems which are very vital at the present time. The purpose of this paper is to review briefly a few of the more important trends, methods, and developments of the past eight years.

Excepting in Germany and possibly Italy, investigators are coming more and more to realize the necessity of and the problems involved in a strictly scientific method of investigation. Investigators are becoming sceptical about the existence of a primitive man in the proper sense of the word. Practically all recent studies lead to the conclusion of Franz Boas that the mind of man is universal, as well as perennial, since prehistoric times. The differences are in nurture and culture. Garth, in his book *Race Psychology* (1931), undertook a general summary of the findings of experimental attack on the subject. He says that while it may be easy to state the problem of race psychology, it is difficult to control the factors. First it is hard to find representative samplings of the two races to be compared; it is difficult to find a measuring device fair to both, and it is extremely difficult to equate the factors of nurture in the two races studied. After inquiring into the results of many and varied tests, he concludes that we have never laid bare any mental traits which might be called racial; that any differences so far found can and should be laid at the door of nurture and not to racial nature. Other authors, Klineberg, Anastazi, Freemen, etc, have since reached somewhat similar conclusions.

A number of tests have been given to determine whether race differences exist in sensory acuity and in body development. For example, Eells, in 1933, found the Eskimos and Aleut generally inferior to the American Whites in tests of keenness of hearing and in the Seashore musical talent tests, but there was great variability in the groups. The inferiority was attributed to the drastic experiences of the Alaskan child, due to a rigorous climate and long periods of inactivity. A large number of different racial groups have been studied with the Ishihara colour blindness test. Although apparent differences do seem to occur between White males and some other races as the Japanese, it was found in Japan that the colour blindness rate varied radically from one province to another. Evidently the incidence of colour blindness depends on inbreeding, and it may have reached a saturation point among White males in America where we find the largest incidence of 8 %.

No less than seventy studies of the problem of racial intelligence have been reported in the last eight years. These have been made with the Binet and other individual tests, and with various group tests, verbal, non-language, and performance tests. The Binet has pretty thoroughly, in some form or other, passed from one country to another. The Goodenough "Drawing a Man Test" and the "Porteus Maze Test" have also

been widely used in the study of race psychology. Klineberg finds, in a study of migrant negroes in New York who came from the south, that the longer they resided in New York the higher their I.Q. became, and that those born in the north have an average I.Q. of about 0·93. This he has shown is not due to selective migration but to cultural and environmental factors.

Except for the emphasis which is continually being laid on euthenics in all studies of intelligence, nothing new has come to light in connexion with studies on the American Indian. It seems evident that the intelligence of the American Indian is handicapped by more than language difficulty. The results of tests in numerous instances of Indian children reared in White homes justify the expectation that euthenics will raise the Indian to the level of the Whites, but these results are not yet available in sufficient number of cases to make them conclusive.

In the study of the intelligence of Nordic, Mediterranean, and Alpine populations in Europe, Klineberg finds a few differences between the groups, but that these are small and unreliable. The French Mediterraneans made the best median score of all. Apparently there is no real basis for the alleged superiority of Nordics.

There are a few studies on racial aesthetics; however, they are too meagre and inadequate to lead very far in revealing conclusions with reference to this subject. They are not inconsistent with the general principle laid down by Boas and others that there are really no different racial aesthetics. The differences in racial art are to be found in materials and virtuosity, and the art principles used by all races are the same. At least eight different studies have been made with the Seashore Musical Talent Tests, but in none of them were definite race differences indicated which could not be explained by the influence of nurture. G. B. Johnson has made an extensive study of the Negro spiritual, and his conclusion is thoroughly consistent with what Boas has said regarding racial art—that it does not exist, that all art is the product of materials and environment.

There have been a few studies made regarding personality due to race; however, since the tests have not been perfected and the nurtural factor has not been controlled, they furnish little or no basis for conclusions regarding racial differences.

95

GATES, R. RUGGLES. ***Blood Groups and Race***

The spread of the blood groups in the history of mankind is one of the most interesting problems in human genetics. Although large numbers of tests have been made in races all over the world, the interpretation of the distribution of the *A* and *B* agglutinogens, as found in the various continents and races, is by no means clear or final. Since the *A* and *B* are inherited strictly as Mendelian units dominant to *O*, we must assume on genetical principles that they have arisen as mutations, *O* being regarded as the primitive condition. It is also necessary to assume that, like other mutations, they occur repeatedly with a certain frequency, which may be of the order of 1 in 100,000. The evidence of their distribution is strongly against any selective action. Their spread would therefore appear to be a result of their mutation frequency and the time which has elapsed since they began to appear. The migration and crossing of races will also of course have important effects in the dispersal of the blood groups.

The widespread presence of *A* in many primitive races indicates its early origin, and its derivation from anthropoid ancestors is not excluded. *B* seems to have begun to appear in man more recently, as a parallel mutation to the *B* found in the orang and gibbon. It is as yet uncertain whether *B* arises from *O* or from *A*. The American aborigines appear to be mostly *O* when of pure blood—a somewhat enigmatic condition, since they are by no means so primitive physically and psychically as the Australian aborigines, who have about 40 % of *A*. The fact that the Blackfoot and related tribes are very high in *A*, however, lends support to the view of local centres of the *A* (and *B*) mutation. This is also in accord with recent evidence that some at least of the mutations of *Drosophila* species are geographically localized.

96

GATES, R. RUGGLES. ***The Geographical Relationships and Evolution of the Subgenus*** **Onagra**

The large amount of genetical work done on the genus *Oenothera* has laid the basis for views regarding not only the mechanisms of inheritance and variation, but also the factors involved in the differentiation of species and the course of phylogeny within the genus. It seems clear that large-flowered uncatenated species such as *O. Hookeri* served as a starting-point. The distribution of these ancestral forms until the end of the Pleistocene would have been in southern latitudes, from Central America and Mexico to the southern States. The development of some seventy-five known species spreading over the North American continent since the retreat of the ice is a rapid evolution. It was accompanied by the development of small flowers and complete chromosome catenation as well as the formation of complexes and other genetic mechanisms characteristic of *Oenothera*. Analysis of most local populations shows a large number of variations be-

longing to one or more species, so that the number of types is endless and many of the species grade into each other.

Beginning in 1932, seed collections have been made from some hundreds of localities, mainly in eastern Canada but partly in the northern States and the prairie region. An astonishing variety of types was disclosed, some of them related to species already known and some with entirely new characters. They show that in some regions a complicated plexus of forms exists, in which specific delimitation is necessarily somewhat arbitrary. Many of the species show large series of variations from one locality to the next. Were the peculiarities of *Oenothera* genetics unknown, many of them might easily be mistaken for simple Mendelian differences segregating in the population.

Certain well-marked species have, on the contrary, been found to occur in a single locality,whereas, so far as is known, only one species occurs throughout Saskatchewan. Forms which cannot be separated from this species are found from the Okanagan Valley in British Columbia to the vicinity of Ottawa and as far east as the Lower St Lawrence.

While the factors for smaller flowers have apparently arisen as a series of dominant mutations, most of the other specific differences appear to have occurred as recessive genic mutations. Among the differences which behave as units in populations may be cited the presence of red or green papillae on the stem, or the absence of papillate hairs (in *O. oakesiana*, and the prairie species); purple spots on the rosette leaves; erect or bent stem tip; red papillae on the sepals; red shoulders to the bud; cruciate petals; red or white midribs; smooth or crinkled leaves; at least four different widths of leaves; large or small bracts; and a number of others. Probably some of these have originated independently through parallel mutation a number of times in different species. As regards flower size, it appears that whereas the original large-flowered species with free pairs of chromosomes gave rise by a series of steps to species with small flowers and complete catenation, there is a secondary effect in some northern latitudes by which segregates arise which have lost some of the dominant factors for very small flowers, and so have flowers of medium size.

97

GEITLER, L. *Polyploide Somakerne und ihre Entstehung durch Endomitose bei Heteropteren*

Die Somakerne der Heteropteren besitzen sehr beträchtliche Grössenunterschiede; für bestimmte Gewebe ist meist eine bestimmte Grösse bezeichnend. Da die Chromosomen im Ruhekern distinkt erhalten bleiben, lässt sich die Ursache der Grössenunterschiede sicher feststellen. Vergrösserte Kerne entstehen auf zwei Wegen: (1) unter Erhaltenbleiben der diploiden Chromosomenzahl durch Kernsaftvermehrung, (2) durch Polyploidisierung. Der (1) Fall spielt nur eine geringe Rolle (manche Ganglienzellen). Der typische Fall ist die Polyploidisierung; so sind bei *Gerris* die Kerne der Hodensepten 16-ploid, der Malpighischen Gefässe 32-ploid, der grössten Speicheldrüsenkerne 1024-ploid.

Die Polyploidisierung erfolgt durch *Endomitose*. Ihr wesentlicher Unterschied gegenüber der gewöhnlichen Mitose besteht darin, dass keine Spindel ausgebildet wird und dass im Zusammenhang damit alle gerichteten Bewegungen der Chromosomen, also Bildung einer Äquatorialplatte und von Tochterplatten, unterbleiben. Der Formwechsel der Chromosomen selbst (Spiralisierung) ist dabei fast der gleiche wie während der Mitose; sie durchlaufen also eine Endoprophase, Endometaphase, Endoanaphase und Endotelophase. In der Endometaphase wird der Längsspalt erkennbar und die Chromosomen sind maximal, aber nicht so stark wie in der gewöhnlichen Metaphase, verkürzt, in der Endoanaphase beginnen sich die Chromatiden zu trennen, in der Endotelophase rücken sie vollends auseinander. Die endoanaphasische Bewegung erfolgt unter parallelem Auseinanderweichen der Chromatiden ohne sichtbare Beteiligung der Centromeren, also grundsätzliche gleich wie im Fall der Colchicinmitose.

Auf diese Weise erfolgt das Wachstum der meisten Gewebe während der larvalen Entwicklung. Auch das erneuerte Epithel des Mitteldarms der Imago wächst unter Endomitosen. Zellvermehrung unter Erhaltenbleiben der Diploidie ist dagegen für die Epidermis und das Nervensystem bezeichnend.

Das cytologische Bild der polyploiden Kerne erfährt bei verschiedenen Arten durch die Beschaffenheit der Geschlechtschromosomen bestimmte Modifikationen. Im Fall des *XO*-Typus bestehen zwei Möglichkeiten: ist das *X*-Chromosom relativ sehr gröss, so ist es somatisch heterochromatisch (durch Auszählen der *X*-Chromozentren lässt sich die Polyploidiestufe unmittelbar feststellen); ist es relativ klein, so fehlt somatische Heterochromasie. Im Fall des *XY*-Typus ist allein das *Y*-Chromosom im Soma heterochromatisch (Pentatomiden, Capsiden); in den polyploiden Kernen bilden die *Y*-Chromosomen meist ein grosses Sammelchromozentrum. Es ist wahrscheinlich, dass das Heterochromatin unwesentliche Ballastsubstanz ist.

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98

GEYER, H. ***Die Erbpathologie der Geschwülste des Zentralnervensystems und seiner Hüllen***

Die bisherige Betrachtung der Blastome des Zentralnervensystems und seiner Hüllen ist von histologischen, morphologischen, diagnostischen und therapeutischen Erwägungen ausgegangen. Eine genetische Betrachtung dieser Neubildungen ist nur ganz vereinzelt vorgenommen worden. Die bisher vorliegenden Ergebnisse der Familienforschung sowie der Zwillingsforschung konnten durch eigene Untersuchungen gemeinsam mit Pedersen wesentlich erweitert werden. Es wird über die bereits veröffentlichten Tatsachen auf dem Gebiete der Erbpathologie der Hirngeschwülste zusammenfassend berichtet, und ein erster Versuch gemacht zu genetischen Abgrenzungen zu gelangen. So kann nunmehr in der Gruppe der Glioblastomatosen eine erbliche und eine nichterbliche Gruppe unterschieden werden. Ein weiterer fruchtbarer Gesichtspunkt wissenschaftlicher Betrachtungsweise wird durch die Einführung der von *Lenz* und *Withman* aufgestellten Theorie der somatischen Mutation als Ursache von Gewebsneubildungen gewonnen.

99

GHIGI, A. ***Genetics of Cerebral Hernia in the Fowl***

In three series of experiments a bantam breed with cerebral hernia has been produced; in a first mating of Padua cock with Java and Sebright hen, the Bantam Ghigi was obtained. This was then backcrossed with Java and Sebright bantam. The offspring from these matings were available for the following studies: An anatomical and embryological study of cerebral hernia; biometrical study of the population with hernia of hybrid origin; a biometrical study of the effects of selection on the brains of the progeny from backcrosses of Ghigi bantams with Java cockerels and Sebright hens. Theoretically, three generations, beginning with F_2, are necessary for producing in nearly all the birds a hernia, which is fairly uniform and varies within a narrow range. One more generation is necessary if the F_2 is not accessible for selection, and one generation less if the F_2 contains specimens which possess several positive genomeres. The cerebral hernia caused by an elongation of the brain is a recessive and polymeric character.

100

GHIGI, A. ***Interspecific Crosses in Pheasants***

The experiments of the author on the crosses between silver pheasant (gen. *Gennaeus*) and golden pheasant (gen. *Chrysolophus*) may now be considered as complete.

The F_1 hybrid males are entirely fertile.

The females are all sterile, but their external appearance and the conditions of the gonads are individually variable.

The females derived from the backcrosses between hybrid male and golden female are all uniform and have normal appearance; the females derived from the backcrosses between hybrid male and silver female, show a variability like the F_1 females, oscillating between phenotypically and gametically normal individuals, and others which are intersexuated and masculinized in their exterior appearance.

The females derived from the backcrosses of the hybrid male *Syrmaticus reevesi* × *S. soemmeringi* with *reevesi* ♀ show a phenotypic intersexuality like those of the first generation; hence *S. soemmeringi* is not a *Syrmaticus* and its systematic position should be corrected.

The backcrosses between *Diardigallus* and *Gennaeus*, and between *Lophura* and *Gennaeus* give fertile females, whereby is demonstrated the greater gametic affinity between the subgenera of the old genus *Euplocomus*.

101

GINI, C. ***Considerazioni a cui danno luogo i caratteri concatenati a seguito dell' intercambio***

Chiamiamo cromatidi *derivati* i cromatidi ottenuti a seguito dell' *intercambio* (*crossing-over*) in contrapposto ai cromatidi originari.

È evidente che, se i cromatidi derivati sopravvivono e si moltiplicano come i cromatidi *originari*, l' intercambio tenderà a far sempre aumentare il numero dei cromatidi originari, e questi, se non intervenisse nessun compenso, tenderebbero a divenire la forma generale della popolazione. C' è però un compenso nel fatto che i cromatidi derivati possono, a loro volta, presentare intercambi che ricostituiscono i cromatidi originari e tendono cosi a diminuire la frequenza dei cromatidi derivati. Sotto l' influenza di queste due opposte tendenze, una condizione di equilibrio stazionario viene a determinarsi, nella quale la frequenza dei cromatidi originari e dei derivati rimane costante.

L' autore ha esaminato particolarmente il caso di due fattori α e β aventi sede nello stesso cromatide e

quindi concatenati, ciascuno dei quali ammotte due alleli, rispettivamente **A** e **a** e **B** e **b**, uno dominante (**A** e, rispettivamente, B) ed uno recessivo (a e, rispettivamente, **b**). Rispetto ad essi, si potranno quindi distinguere due cromatidi originari e due cromatidi derivati a seguito dell' intercambio. Ora, se con p, q, r, s, si indicano le frequenze dei quattro cromatidi **AB**, **ab**, **Ab**, **Ba**, e con F_{I}, F_{II}, F_{III}, F_{IV} le frequenze dei rispettivi fenotipi, si dimostra che, sotto le ipotesi che i cromatidi originari abbiano la stessa probabilità di sopravvivere, di moltiplicarsi e di presentare un intercambio, si ha equilibrio stazionario, in regime di panmixia, quando si verifichi l' uguaglianza:

$$pq=rs$$

da cui segue:

$$F_{\mathrm{I}}F_{\mathrm{II}}=F_{\mathrm{III}}F_{\mathrm{IV}}$$

e ciò, sia che i cromatidi originari siano **AB**, **ab**; sia che originari siano **Ab**, **aB**. Si dimostra anche che tale equilibrio è, non solo stazionario, ma anche stabile, cosicchè, una volta turbato, tende a ristabilirsi.

Nel caso che i cromatidi originari fossero **AB** e **ab**, sarebbe

$$p=q, \quad F_{\mathrm{III}}=F_{\mathrm{IV}};$$

nel caso che cromatidi originari fossero **Ab** e **aB**, sarebbe:

$$r=s \quad \text{ma non} \quad F_{\mathrm{I}}=F_{\mathrm{II}}.$$

I due casi non sono dunque perfettamente simmetrici.

In pratica le forme risultanti dall' intercambio sembrano essere meno frequenti delle originarie, e talvolta addirittura eccezionali. Cio fa pensare che le ipotesi sopra enunciate non rispondano al vero. Si dimostra a tal proposito:

(1) Che qualora vi sia omogamia tra i fenotipi, purchè vi sia omogeneità nella popolazione, ferme restando le altre ipotesi, si ha sempre:

$$F_{\mathrm{I}}F_{\mathrm{II}}=F_{\mathrm{III}}F_{\mathrm{IV}}.$$

(2) Che qualora vi sia eterogeneità nella popolazione, ferme restando le altre ipotesi, si ha:

$F_{\mathrm{I}}F_{\mathrm{II}}>F_{\mathrm{III}}F_{\mathrm{IV}}$ se i cromatidi originari sono **AB** e **ab**, e $F_{\mathrm{I}}F_{\mathrm{II}}<F_{\mathrm{III}}F_{\mathrm{IV}}$ nel caso contrario.

Si mostra pure, anche servendosi di esempi, che l' influenza di tale eterogeneità è limitata e non certo sufficiente a dar ragione della differenza che si presenta in pratica tra $F_{\mathrm{I}}F_{\mathrm{II}}$ e $F_{\mathrm{III}}F_{\mathrm{IV}}$.

Applicazioni vennero fatte al caso del colore dei capelli e degli occhi nella razza umana, nell' ipotesi (che pare plausibile) che essi dipendano da fattori concatenati. È risultato che le due categorie di individui eterocromi (capelli scuri — occhi chiari; capelli chiari — occhi scuri) e più la seconda che la prima, presentano una frequenza molto minore di quella che un equilibrio stazionario comporterebbe.

Non pare però che tale minore frequenza dipenda da una minore resistenza vitale o da una minore prolificità degli individui eterocromi, cosicchè si potrebbe concludere che la loro frequenza dipende da una minore attitudine dei corrispondenti cromatidi derivati a sopravvivere o a riprodursi nello stato di gameti o di zigoti.

102

GINI, C. ***The Relative Importance of Hereditary and Non-hereditary Factors in Determining the Heterogeneity of a Generation***

Four methods are so far used for measuring the relative importance of hereditary and non-hereditary factors in determining the heterogeneity of a generation: (I) parental correlation, (II) fraternal correlation, (III) comparison between identical twins reared in different environment and children of different parentage reared in the same environment, (IV) comparison between the different categories of twins, and between them and ordinary brothers and non-related parents. All these methods are useful, but all have also their shortcomings.

Two more methods (V) and (VI) are suggested in this paper, which are far from being perfect, but may present some advantages.

The first method (V) is very simple, so simple that it would be only natural that it should have been proposed and used in the past; but, so far as I know, it has not so far been suggested.

If v is the variance of a character in a generation and v_w the variance of the said character within fraternities, and we admit (hypothesis A) that the non-hereditary factors acting within fraternities are independent in their actions and in their effects from the factors acting between fraternities, the expression

$$E=1-\frac{v_w}{v}$$

gives a measure, approximate for excess, of the relative importance of hereditary factors in determining the heterogeneity of the generation.

Really E does not give the relative importance of hereditary factors, but the relative importance of hereditary factors plus such part of non-hereditary factors whose effect is felt between fraternities and not within fraternities.

The relations between E and the coefficient of parental and fraternal correlation have been examined.

An alternative method (VI) of determining E may be used when we know: (*a*) the differences within fraternities, as well as (*b*) the differences between

children of different fraternities having both father and mother phenotypically identical for the character considered.

Calling Δ_w the mean square of the differences (*a*), Δ_b the mean square of the differences (*b*), Δ_m the mean square of the differences between the fraternity averages, and k the average number of children per family, and admitting (hypothesis B) that the variability within fraternities is independent from its size, we obtain approximately

$$\Delta_b = \frac{k-1}{k}\,\Delta_w + \Delta_m .$$

But Δ_w measures the heterogeneity due to non-hereditary factors acting within fraternities; Δ_b measures the heterogeneity (due to all the factors, hereditary and non-hereditary) of the children of different fraternities having both father and mother phenotypically identical. So the difference

$$D_w = \Delta_b - \Delta_w = \Delta_m - \frac{1}{k}\,\Delta_w$$

may be taken as the measure of the heterogeneity of children of parents phenotypically identical due either to hereditary factors or to non-hereditary factors acting only between fraternities.

Now, admitting the hypothesis A, and furthermore the hypothesis (hypothesis B) that the amount of heterogeneity of children of parents phenotypically identical, due either to hereditary factors or to non-hereditary factors acting only between fraternities, is equal to the amount of heterogeneity of children phenotypically identical, due to the same factors, we obtain

$$\frac{D_w}{\Delta_w} = E,$$

which allows us to calculate E, knowing Δ_w, Δ_b and Δ_m.

This method (VI) may be used as a substitute to method (V) when we do not know v for the whole generation, or as a control when, knowing v, both methods are applicable.

When, however, both methods (V) and (VI) are applicable, the first is preferable because:

(*a*) it is simple;

(*b*) it is not bound to hypothesis B (a natural hypothesis, but which may become dangerous when the data are not numerous) and to hypothesis C (also a natural hypothesis, but which may be in defect in special cases);

(*c*) the number of fraternities for which Δ_b can be determined may be more restricted than the number of fraternities for which v can be determined;

(*d*) the definition of individuals phenotypically identical is inevitably arbitrary; moreover, it is impossible in practice to establish, for several different characters, the intervals between which the individuals are to be considered identical, in such a manner that they be equivalent and consequently the results be exactly comparable. It would be necessary, for that purpose, to establish, not the same interval for all the characters, but intervals proportional to the respective standard deviations; but generally the data are already collected with the usual classification in mm. or cm. or kg., and also when they still have to be collected it would be impracticable to follow, for the majority of characters, a different system, taking account of the construction of the instruments employed.

Data for application of methods (V) and (VI) are easy to collect but so far they are very scarce.

The only data for man that I succeeded in finding are those—rather restricted in number—elaborated by R. A. Fisher and H. Gray, based on Boas material on Sicilian immigrants to the United States. In the next table the results obtained on them are reported, together with the paternal and maternal coefficients of correlation and their average.

Characters	Relative importance of hereditary factors according to the methods				
	V	VI	I		
			Paternal coefficient of correlation	Maternal coefficient of correlation	Average parental coefficient of correlation
Width of head	0·48	0·62	0·37	0·34	0·35
Width of face	0·46	0·53	0·36	0·31	0·33
Length of head	0·35	0·28	0·30	0·33	0·32
Stature	0·30	0·13	0·29	0·33	0·31

The discrepancies between the results obtained by method (VI) and those obtained by the more reliable method (V) are very strong. However, they agree in showing that the relative importance of hereditary factors differs for the various characters, and both methods give for these characters the same order according to the importance of heredity (width of head, width of face, length of head, stature). The discrepancies may be explained by the rather restricted number of fraternities considered as well as by the incertitudes of method (VI) due to the circumstances above mentioned under (*b*), (*c*) and (*d*). Circumstances (*d*) may in particular explain, at least partly, the higher values for width of head and width of face and the lower values for length of head and stature obtained by method (VI) in comparison with those obtained by method (V).

Moreover, it is to be remembered that Fisher and Gray did not operate on the observed data (which, referring to different age, are not comparable) but to

the data corrected for age by means of lines of regression, a correction which, on the one hand, was indispensable, but, on the other, inevitably introduces an element of incertitude which may contribute to the said discrepancies.

The paternal and maternal coefficients of correlation are much more uniform for the different characters in comparison not only with the results obtained by method (VI) but also with those obtained by method (V). Generally (in seven cases out of eight) they are lower than the results obtained with method (V), which does not run counter to expectation. Their averages, however, show the same order of the relative importance of the hereditary factors for the different characters.

Methods (V) and (VI) may be applied also to groups larger than families for which the hereditary factors may be considered the same: in these cases the approximation of the two methods is better, because the part played by the non-hereditary factors acting between the groups and not within the groups is more reduced. This is the case for the so-called "pure lines" represented by the descendants, obtained by self-fertilization, of the same individual. This seems a field proper for the application of the above-proposed methods.

So it is odd that Johannsen seems not to have thought of it, in spite of the criticism to which he subjected the correlation coefficient as a measure of heredity. His researches furnish, however, appropriate material for the application of method (V). From a re-elaboration of his data on 5494 seeds of *Phaseolus vulgaris nana*, related to nineteen pure lines, I obtain

$$E = 0{\cdot}331.$$

Johannsen, on the same data, had calculated the value of the correlation coefficient obtaining $r = 0{\cdot}336$. In this case the methods (I) and (V) give almost identical results.

This coincidence is in contrast with the discrepancies between the results obtained for man. But it is to be remembered in this connexion that, in the pure lines of Johannsen, the ancestor of the pure lines was a perfectly homozygous individual.

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Gisquet, P., Dufrenoy, J. and Dusseau, Mlle A. *Interspecific Hybrids among* Nicotiana*; Hybrids between* N. Tabacum *var.* purpurea *and* N. petunioides *var.* sylvestris

Purple-flowered *Nicotiana Tabacum purpurea* and white-flowered *N. sylvestris* are representatives of two different species of *Nicotiana*, *N. Tabacum* with 24_{II}, the latter with 12_{II} chromosomes.

According to Clausen and Goodspeed, the 24_{II} of *N. Tabacum* are made up of the whole complement of the assumed parent *N. sylvestris* and the whole complement of the other assumed parent *N. tomentosa*.

The F_1 hybrid *purpurea* × *sylvestris* displays most of the characters of *N. purpurea*, with a touch of *sylvestris* in the appearance of the various organs; it shows heterosis vigour, it blooms profusely for a long while, but most of the flowers drop; a few may set into shrunken capsules which drop before they mature, and seem to contain but a few empty seeds.

Pollen mother cells at first metaphase show quite a variable number of bivalents or univalents; unpaired or variously clumped chromosomes may lag not only out of the plate but even out of the spindle. However, counts may be obtained of 18_{II}. Gisquet, Directeur de l'Institut expérimental des Tabacs at Bergerac (France), as early as 1924 had reported obtaining a few good seeds from F_1 from which he obtained descent down to the F_{13}.

F_2 hybrids segregate as to earliness, size, growth habit, leaves and flower colour.

Sectoring on leaves and flowers discloses the unbalanced chromosomal condition even in most of the hybrids which survive: these hybrids could be selfed, and yielded a number of genotypes.

At each successive generation, any of these genotypes built up a more homogeneous and more fertile population, from which it could be inferred that unpaired univalents were progressively left out at meiosis, and thus a well-balanced genom was built up.

Among genotype (48), pollen mother cells, at the F_2, still show a proportion of abortion; equatorial plates at first metaphase show a varying number of bivalents.

From practically sterile interspecific hybrids, new fertile *Nicotianae* were obtained, combining permanently characters from both parental species.

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104

Gökğöl, M. *Zur Frage des Ursprungsgebietes der Weizen*

Die Genzentrentheorie verlegt den Ausgangspunkt einer Art in den Bezirk grösster Variabilität. Der Verfasser unternahm eine Analyse der Weizen-Arten und Unterarten, um das Ursprungsgebiet für die verschiedenen Weizen-Varietäten zu bestimmen. Für die diploide Gruppe wird allgemein Anatolien als Urheimat anerkannt. Als Ausgangspunkt der tetraploiden Weizengruppe (*dicoccum* and *durum*) sieht er Anatolien (Kleinasien) an. *Triticum dicoccoides*, die

Wildform der tetraploiden Gruppe tritt in Toros (Anatolien) auf, ist hingegen unbekannt in Abessinien. *T. polonicum* und *turgidum* werden von *durum* abgeleitet. Von den 72 bekannten Varietäten von *turgidum* wurden nicht weniger als 48 in Anatolien nachgewiesen. Von *polonicum* enthält die abessinische Gruppe 6 festgestellte Varietäten, die mediterrane 34, von denen 6 neu in Anatolien gefunden wurden. Das Fehlen von zwei Varietäten von *T. durum*, nämlich *abessinicum* und *expansum*, in Kleinasien sowie die Tatsache, dass keine Formen mit blau-violetten Körnern oder mit unbegrannten Ähren in Kleinasien gefunden wurden, wird vom Verfasser nicht als Widerspruch zu seiner Theorie angesehen. Seiner Ansicht nach sind diese Formen viel später unabhängig aus den anatolischen entstanden.

Die ältesten Formen finden sich in der *vulgare* und *compactum* Gruppe (hexaploider Weizen). Von 270 *vulgare* Formen wurden 223 in Anatolien festgestellt, und von 137 *compactum* Formen sind 100 in Anatolien bekannt.

Der Verfasser kommt somit zu dem Schluss, dass es für die Weizenarten nicht mehrere von einander getrennte Ursprungsgebiete gibt, sondern nur ein einheitliches, nämlich Vorderasien: Anatolien, Syrien, Palästina, Südkaukasus und die an Anatolien angrenzenden Teile von Persien. In dem genannten Gebiet finden wir nicht nur ein der Vavilovschen Theorie entsprechendes Mannigfaltigkeitszentrum für die diploiden, tetraploiden und hexaploiden Weizen, sondern gleichzeitig treten hier auch die beiden Wildformen *T. aegilopoides* und *T. dicoccoides* auf. Zuletzt darf nicht unerwähnt bleiben, dass auch alle Vorbedingungen für die Entstehung der hexaploiden Weizen gegeben sind, ganz gleich welche Hypothese hier die richtige ist.

105

GORDON, C. and SANG, J.H. ***The Effect of Environment on the Exhibition of the Mutant "Antennaless" in*** **Drosophila melanogaster**

The mutant antennaless in *Drosophila melanogaster* appeared in a roughoid (3,00) eyed stock originally derived by inbreeding. The exhibition of the character was found to be high among flies which emerged early. It fell steadily to a minimum at about the sixth day, and then rose steadily, till, in some instances, it exceeded the initial level. Exhibition is also affected by the gene complex. Selection for high exhibition has resulted in strains with initial exhibition of 98 % having the same general type of variation curve for exhibition frequency and time of emergence. Preliminary localization tests have shown antennaless to be on the second chromosome.

The form of the time-exhibition graph corresponds closely to the curve for the *p*H of the medium as determined by Bridges and Darby, with transfer of origin corresponding to the time taken for development of the adult.

Experiments were first designed to find out whether *p*H, (*a*) directly or (*b*) indirectly by changing (1) the quantity or (2) the quality of the yeasts present, affects the exhibition of the character. Strains used had been pure-lined for at least forty generations. Buffering the ordinary maize-meal-treacle medium altered the exhibition in the direction anticipated on the theory that exhibition depends on hydrogen-ion concentration. However, *p*H was found to have no direct effect on the phenotypic index of flies grown on highly buffered, sterile media. So far there is no indication that food quantity has any influence on the expression of the gene. Different strains of yeast are found to be more or less propitious to the exhibition of the gene, and it appears that the yeast itself contains a substance which inhibits antenna growth. This substance acts early in larval life.

In so far as changing hydrogen-ion concentration of the food medium contributes to the form of the emergence graph it can do so only by qualitative selection of the yeast population.

106

GORER, P.A. ***Transplantation and the Differentiation of the Malignant Cell***

The conclusions to be stated below are based for the most part on experiments performed on pure lines of mice, but are probably of general applicability. When normal or malignant tissues are transplanted within a pure line persistent grafts are obtained in the great majority of cases, whilst when transference is made to unrelated animals the graft is usually destroyed after a somewhat variable lapse of time. It has been shown that the reaction resulting in destruction of the graft is elicited by genetically determined factors present in the grafted fragment but absent in the host. Evidence has been obtained in support of the view that the defensive reactions mentioned above have much in common with those determining immunity to infection with micro-organisms and have been termed iso-immune reactions, the substance eliciting the reactions being termed *iso-antigenic factors*.

Genetic experiments indicate that tumours differ widely from one another in the number of iso-antigenic factors they possess, and further that such factors may be lost suddenly during the course of transplantation. The number of factors as estimated genetically for mammary cancers appears to vary from one to ten.

Recent work has shown that the following points must be taken into account in the assessment of data obtained by purely genetic means:

(1) Evidence obtained from a variety of sources indicates that tumours possess to a variable extent the faculty of neutralizing the defensive reactions of the host, very exceptionally to a degree that permits growth in spite of interspecific differences but more commonly in spite of iso-antigenic differences.

(2) There can be little doubt that iso-antigenic factors differ considerably from one another in their ability to elicit a defensive reaction.

(3) Serological experiments suggest that the amount of one (or possibly more than one) iso-antigenic factor may be considerably *increased* in the malignant cell; this would probably result in the partial or complete masking of several other factors. Should this increase take place in such a way as to favour a relatively ineffective factor a considerable loss of specificity might occur.

The above points suggest that purely genetic experiments would tend on the whole to exaggerate the number of factors lost by malignant cells. This statement might appear to favour the idea that the cancer cell arises by somatic mutation. The genetic evidence taken at its face value demands that the simultaneous occurrence of homozygous mutations at five or six loci should be a relatively common event. The masking of several factors by the hypertrophy of a single factor makes fewer demands on the mutation rate. However, normal tissues differ from one another in the intensity of the reactions they elicit when grafted. They also differ from one another both quantitatively and qualitatively in the iso-antigenic factors they contain. It therefore appears justifiable to regard the malignant cell as arising by anomalous differentiation.

107

GORER, P.A. *The Question of Dominance in Spontaneous Cancer*

Before discussing the question of the dominance of spontaneous cancer it is important to decide whether animals fall into two classes with regard to a given tumour. So far as mice are concerned it is probably not so. Susceptibility of pure lines to mammary cancer may take almost any value from less than 1% to more than 80 %. The same is almost certainly true of lung cancer and probably of liver tumours and leukaemia.

There is ample evidence to justify the statement that various types of tumours occurring in any one species may differ widely in their genetic basis. Furthermore, it is a commonplace of genetics that the degree of dominance of any gene may vary in different crosses. In the case of cancer in the mouse it is not as yet possible to use crosses with the wild type as a standard of reference. For these and other reasons it is not permissible to generalize concerning the dominance of genes producing cancer even in a single species.

The great bulk of reliable work on the genetics of mammary cancer in the mouse has established the importance of some maternal influence that the latest work shows to be transmitted in the milk. Elsewhere, evidence has been presented that suggests the existence of genes influencing susceptibility to the milk-borne agent, but it is premature to discuss the question of their dominance. Since leukaemia in the mouse also shows a maternal effect the question of dominance must also remain in abeyance.

Lung cancer in the mouse shows Mendelian inheritance, and the following points must be taken into account in considering its genetic basis:

(1) Most lung tumours appear to be relatively benign and slow-growing. It is probable that their first appearance may antedate death by some months. Tumours found post-mortem are frequently completely dissociated from the cause of death. In one cross between two contrasted pure lines the tumours are found later in the hybrids than in the high-cancer parent, but are usually much larger than in the pure line.

(2) There is some evidence that the appearance of lung tumours is conditioned by three or four genes with an additive effect. If this is so the degree of dominance shown by lung tumours may depend upon the number of genes introduced by the high-cancer parent. Dominance modifiers may produce further complications.

(3) In those cases where the onset of the tumours is delayed in the heterozygote, with or without a corresponding alteration in the total incidence, it is probably incorrect to speak of a change of dominance with age (as done by Bernstein), since it is likely that the reactions preceding the appearance of the tumour simply occur more slowly in the heterozygote (as suggested by Goldschmidt in analogous cases).

In animals other than the mouse some of the genes favouring the appearance of tumours are partially dominant (e.g. melanomata in *Platypoicoelus* hybrids, the melanomata of grey horses, *polyposis intestini*, and neurofibromatosis in man), others are recessive such as xeroderma pigmentosum in man and various tumours in *Drosophila*.

108

GOULDEN, C.H. *Problems in Plant Selection*

This is a general discussion of the problems of plant selection from progenies of crosses between self-fertilized plants. For illustration, some of the diffi-

culties encountered in wheat breeding are outlined. The chief purpose of the paper is to outline some of the ways in which statisticians, by making theoretical and practical studies of specific problems, may be of considerable assistance to the plant breeder.

In wheat breeding there are two main objectives. The first is to obtain true-breeding lines by selection from the hybrid progenies; the second is to select from these lines, those that have the desired combination of characteristics. The methods of breeding that are now employed are based on the principle that progress in obtaining the lines having the desirable characters can be made at the same time as the lines are being selected for homozygosity. This requires that the progenies of single plants selected each year be grown under conditions representative of those for which the new varieties are being developed, and that the progenies be large enough so that certain tests for desirable characters can be made. This means that, with the exception of the F_1, only one generation can be grown each year. If it were possible to separate the two phases of breeding, the first step would be to reach homozygosity in as many lines as possible. The progenies of single plants could be cut down to a minimum of one or two plants, and two generations could be grown in the greenhouse during the winter and one in the field during the summer. The F_6 generation could be reached in two years, whereas under the system now being used it takes at least five years. After reaching homozygosity in a large number of lines, these could be tested for the desirable characters in an efficient manner by means of the methods that have been devised by Yates for testing large numbers of varieties.

The alternative methods mentioned above require theoretical and practical scrutiny in order to determine which of them is the most efficient and which the most rapid. On the basis of such studies it should be possible to determine the most efficient method for general breeding work.

A problem of lesser importance arises in the procedure of testing a large group of varieties. With respect to yielding characteristics, we can make reliable tests without too great an inflation of the error by using the quasi-factorial and incomplete block methods, but in doing so the method to be followed in evaluating the varieties for other characteristics such as strength of straw, disease resistance and milling and baking quality, is not quite so clear. Quality, for example, cannot be determined on each plot, and consequently the determinations must be made on a composite sample from all of the plots of any one variety. In this respect, therefore, if soil variations have an effect on quality, the differences between the varieties are partially confounded with the blocks. Again, in the final selection of a group of lines, it is not only yield that counts but a general rating based on all characters. After obtaining data on all of the points, what is the most efficient method of combining the data in order to give a rating which can be used as a basis of selection?

109

GOWEN, J.W. *Behaviour of Viruses and Genes under Similar Stimuli*

Much of our evidence on the physical attributes of genes comes from experiments using agents capable of extensive rearrangements of chromosomes as well as reorganization of the genes. The fact that a gene is in a fixed position in the inheritance matrix and that this position may affect the gene's expression consequently obscures the interpretation to be attached to such experiments. A material which offers the self-reproducing properties of genes but has the advantage of possible isolation away from any matrix is found in a virus affecting the tobacco plant.

Under natural conditions this virus has a low rate of mutation comparable to that of a gene. The mutations observed in our control experiments show that one type of virus is capable of changing to an entity capable of causing distinctly different effects on the tobacco plant. Over the whole range of observed changes half a dozen types are easily recognized, each type possibly being further separable. With the virus as a particle free of any matrix comparable to a chromosome sheath, it seems unlikely that position effects or the breaking up of a massive chromosomal organization are responsible causes for these changes. The virus results consequently point to the likelihood that genes under similar circumstances are discrete, and separable in their effects from those of their neighbouring genes.

Introduce a pure virus into host plants genetically purified and the results are the same throughout the different plants. If a pure virus is introduced into a genetically different host the observed action may be very different, a change from a generalized to a highly localized disease being one observed effect. The virus expression is affected by the genetic substrate of the material with which it must work, just as the gene is influenced by its substrate.

The virus particle, when exposed to the action of radiant energy of the X-ray or ultra-violet, is inactivated. The form of the inactivation curve is the same as that for single genes, the type being explicable by one absorption of energy being sufficient to cause a change. These changes are unaffected by presence or absence of contaminating materials indicating a direct effect of the energy. The changes are not influenced by the temperature of the virus particle during irradiation.

The wave-length of the radiant energy may influence the result. The size relations of virus particles determined from X-rays of different wave-length are in fair agreement within themselves and with those indicated by other approaches, suggesting that this method used on genes may lead to valid results (Gowen and Gay, 1933). In mutation the virus particle appears to reorganize internally rather than to split or polymerize.

REFERENCE

GOWEN, J.W. and GAY, E.H. (1933). "Gene number, kind and size in *Drosophila*." *Genetics*, 18, 1–31.

110

GREENWOOD, A.W. *A Study of Fecundity in the Domestic Fowl*

Among the many investigations that have been undertaken to search for measurable inherited traits related to fecundity in the domestic fowl attention has been concentrated to a considerable extent on the factor of persistency in egg production. Reproductive activity is a cyclic phenomenon terminated annually in the majority of fowls at the onset of the moulting of the plumage in the late summer or autumn months.

Basing their views on the behaviour of families Goodale and Sanborn (1922) suggest that this characteristic cessation of production at the end of the pullet year has a genetic foundation. Confirmatory observations by Hurst (1925), Hays (1936), and Knox, Jull and Quin (1935) all lead to the generally accepted conclusion that persistency is inherited.

Starting from this premise the data on persistency of egg production in the Institute flock of Brown Leghorns collected over a number of years have been analysed in an attempt to determine, not only the intensity of genetic control of physiological processes occurring at the end of the pullet year and known to be susceptible to modification by extraneous environmental influences, but also by reference to behaviour in subsequent years to define the extent of the age factor on gene action.

111

GRÜNEBERG, H. *Inherited Macrocytic Anaemias in the House Mouse*

Dominant spotting in the mouse (W_1) is lethal when homozygous, the homozygote being highly anaemic. The new allele W_2 discovered by Little and Cloudman usually survives to maturity. The haematology of W_2W_2 and W_1W_2 has been worked out. The erythrocyte number of W_2W_2 animals is reduced to about 50 % of the normal values in infancy and later increases to about 66 %. The haemoglobin is less reduced, and the colour index therefore raised. The mean erythrocyte diameter and volume is markedly increased (macrocytic anaemia), whereas the mean corpuscular haemoglobin concentration per unit volume of cells is normal. There is a moderate anisocytosis. The resistance of the erythrocytes to hypotonic NaCl solutions is normal. There are no nucleated red cells in the circulation. The reticulocyte percentage is higher than normal at most stages of the life history; the number of reticulocytes per unit volume of blood is, however, reduced, except in adult animals, when it may become very nearly normal. Platelet counts are normal. The white cells are less reduced in number than the erythrocytes, and there is sometimes a relative lymphocytosis. No immature white cells occur in the circulation. W_1W_2 is intermediate haematologically between W_1W_1 and W_2W_2.

W_2W_2 mice kept at low atmospheric pressure are able to increase erythrocyte number and haemoglobin to about the same extent as their normal sibs. The difference therefore persists, though on a higher level. On return to normal pressure, normals and W_2W_2 anaemics return to normal values equally quickly. If a severe secondary anaemia, due to repeated loss of blood, is superimposed over the inherited anaemia of W_2W_2 mice, they are able to recover and regain their previous blood values in the same way as a normal mouse so treated reverts to normal values after the cessation of the blood losses. These experiments, taken in conjunction with the fact that W_2W_2 anaemics and some of the compounds W_1W_2 spontaneously improve their blood pictures as compared with the normals between infancy and adult life, prove conclusively that the anaemia of W mice is not aplastic.

Normal infant mice, when compared with normal adults, show every sign of a macrocytic anaemia, that is to say, they have a smaller number of larger red cells with a high colour index, but a normal haemoglobin concentration per unit volume of red cells. This is a reflexion of the fact that the transition from the megaloblastic erythropoiesis of the foetus to the normoblastic erythropoiesis of the adult takes place largely after birth. W anaemics differ from their normal sibs in precisely the same way as normal infants differ from normal adults. The anaemia of W mice is therefore due to the fact that the transition from megaloblastic to normoblastic erythropoiesis is delayed and remains incomplete.

Attempts to influence the anaemia of W_2W_2 mice by subcutaneous injections of "Liver Extract B.D.H. for intramuscular injection" and of "Campolon-Bayer" were unsuccessful.

112

GULICK, A. ***Analysis of Nuclear Material Obtained by Differential Centrifugation of Finely Powdered Glandular Tissue***

It was first pointed out in 1932 by Max Behrens that almost chemically pure preparations of chromatin material could be obtained by submitting frozen and vacuum-dried tissues to ultrafine pulverization followed by centrifugation out of appropriate blends of carbon tetrachloride and the less heavy organic fluids. In most tissue powders the nuclear fragments can be collected at the bottom as a pure cake, since they have a higher specific gravity than any of the cytoplasmic particles. Certain researches now in progress at the University of Missouri make use of this technique as a starting-point.

Dr Dennis T. Mayer, working with us, investigated the chemistry of purified nuclei from beef thymus glands. The only constituents previously known were the histone and the thymonucleic acid. In his best determinations the histone constituted 34 %, the nucleic acid 27·5 or 34·5 % according to the mode of calculation. Thus more than 30 % still remained to be identified. Considerably more than half of this (av. 19·2 % of the fat-free total) was mixed proteins soluble in acid and alkali, all of them precipitable within their isoelectric *p*H range 5·8–6·2. These included a distinctive sulphur-rich globulin, soluble in 5 % NaCl, precipitated upon removing the salt by dialysis, and coagulable from its salt solution at 92·5° C. Its sulphur content is 1·33 %, contained in some other form than cystine, cysteine, or glutathione. It constitutes 8·78 % of the nuclear substance and contains 25·8 % of the nuclear sulphur. It is not yet clear where the remaining sulphur is located.

We are at present investigating the iron distribution within the cell, using the same separation technique, but observing appropriate special precautions. Peroxidase, which is presumably an iron enzyme, was found by Mayer in both nuclei and cytoplasm. In the pancreas the iron content, approximately 100 μg./g. of the desanguinated, dried, fat-free organ, seems to be located principally in the cytoplasm. But if iron slips in through contamination it rises to large figures in the nuclei.

113

HADORN, E. und RIS, H. ***Zur Entwicklungsphysiologie einer Letalmutante von*** **Drosophila melanogaster**

Zweck der Untersuchungen war festzustellen, in welcher Entwicklungsphase der Letalfaktor der Mutante "lethal-giant-larvae" (lgl; $2 \pm 0{\cdot}0$) seine verderbliche Wirkung auszuüben beginnt, und ob dabei die verschiedenen Organsysteme gleichzeitig und gleichmässig geschädigt werden.

Ergebnisse. Die Larvenstadien werden mit normaler Geschwindigkeit durchlaufen, und die volle Grösse einer verpuppungsreifen Larve wird gleichzeitig mit normalen Kontrollen erreicht. Die Bildung des Puparium wird aber bis zum 7-20-Tage hinausgezögert, weil die Tätigkeit der hormonspendenden Ringrüse fehlt oder unterschwellig bleibt. Ein anatomisch-histologischer Vergleich zwischen lgl-Larven und entsprechenden Kontrollen zeigt, dass auch eine Reihe von anderen Organen durch den Letalin ihrer Entwicklung gehemmt werden. Dazu gehören die Speicheldrüsen, die Gonaden und die Imaginalscheiben, besonders die Augen-Antennenscheibe. Transplantationen in normale Wirte ergaben, dass die Entwicklungspotenzen der gehemmten Organe in verschiedenem Masse unterdrückt sind; so entwickeln sich die Ovarien aus lgl-Larven im normalen Wirte weit über dasjenige Stadium hinaus, das sie im letalen Organismus je erreichen könnten, während lgl-Hoden sich trotz Transplantation nicht weiter entwickeln. Diese organspezifisch-differentielle Auswirkung des Letalfaktors kann bedingt sein entweder durch eine primär ungleichmässige Beteiligung des mutierten Locus an den entwicklungsphysiologischen Vorgängen in verschiedenen Organen oder durch unterschiedliche Empfindlichkeit dieser Prozesse in bezug auf die allgemeine Störung.

114

HAGEDOORN, A.L. ***Concentration of Effort in Selection by Means of the "Nucleus Plan" of Breeding Farm Livestock***

The two chief objectives in selection are a constitution which makes the animal yield a profit over expenditure, and uniformity within the groups, i.e. homozygosity in respect of valuable genes and absence of undesirable ones. Breeders are now awakening to the need of selecting according to genotype: progeny testing has come to stay. But the change to the safer selection according to genotype means a complete revolution in animal breeding.

The chief principles are: (*a*) The number of males used in every generation in polygamous animals has an enormous influence upon the reduction of variability. The proportion of heterozygosity (potential variability) of the group which is lost in one generation, approximates $\frac{1}{8}M$ (where M is the number of males used). (*b*) When in one generation only males homozygous for any given gene are used, the percentage of animals heterozygous for that gene in the

next generation is halved, and the number of recessives in the second generation is reduced to one-quarter. (*c*) The number of males used in a polygamous animal is small and can be easily reduced still further by introducing rational methods, e.g. artificial insemination. (*d*) The smaller the number of males selected, the stricter can be the tests for a few proven prepotent, homozygous sires. Even where progeny testing of males is recognized to be of great importance, an enormous number of untested sires remain, so that the proportion of valuable to second-rate gametes can only be improved at an exceedingly slow rate.

In plant breeding, the efforts in selection for the production of commercial seed are concentrated on a very small nucleus, the progeny of a very few progeny-tested individuals, the "elite" seed being propagated for sale and agricultural use.

In reorganizing the breeding of livestock, we should avoid letting the effect of a few progeny-tested highly homozygous and very desirable males on the breed as a whole be swamped by making them compete in their own generation with untried males.

A plan which I have called the "nucleus scheme" is intended to take the place of the existing more or less haphazard efforts in animal breeding. It consists in the following. A number of breeding males are judged according to the quality of their progeny, care being taken that a random sample of their progeny is examined. Males heterozygous for lethals are rejected, and only a few males are chosen that have produced only highly valuable offspring. Really important qualities are given precedence over show points of speculative correlative value. The male breeding stock used is the exclusive product of those few sires. The rate of reproduction determines whether the males used will be only the sons (e.g. in pigs), or the sons and grandsons (e.g. in cattle) of the tested nucleus sires.

The nucleus scheme serves to concentrate the efforts in selection in the hands of a very few specialists who will have a virtual monopoly of the production of male breeding stock. Isolation of the nucleus protects it against the introduction of harmful lethals and unwanted recessives. It entails a certain amount of inbreeding, with all its benefits and none of its disadvantages. It can be adapted to the present breeding scheme, where a relatively small number of pedigree breeders produce most of the male breeding stock by substituting progeny tests for partial reliance on show points and the individual quality (phenotype) of the sire's dam. Herdbook societies should co-operate with geneticists to put the breeding of farm livestock upon a rational basis, so that this revolution in methods will work out smoothly and effectively.

115

HALDANE, J.B.S. *Natural Selection in Man*

Apart from mutation and random survival, three processes may cause the frequency of a gene to increase or decrease, namely, natural selection in the Darwinian sense of survival, sexual selection, and reproductive selection, that is to say selection of the most fertile. As regards any particular gene these processes may be antagonistic. The fitness of a given genotype in a given environment is determined by all three, and the three together constitute natural selection in the broadest sense.

At least four types of selective process may be distinguished, at any rate in theory:

(1) Slow selection of genes which cause small increases of fitness, independent of rapid changes in the environment.

(2) Rapid selection of genes causing large increases of fitness, when the environment is changed.

(3) Selection of heterozygotes for certain gene pairs.

(4) Selection tending to eliminate rare mutants which lower fitness.

The first type, exemplified by selection of genes for dark skin colour in the tropics, and of genes modifying dominance, remains hypothetical, though probable. The second type can be exemplified by the selection of genotypes relatively immune to tuberculosis which occurred in Europe in the nineteenth century, and is now occurring in tropical countries. Though the genetical analysis is incomplete, there is little doubt that genes play a part in determining immunity to tuberculosis. Similarly in an age of wars on a national scale such genes as those for myopia increase the fitness of their bearers, and presumably tend to spread. The case is not so clear as regards genes influencing intelligence. Here those responsible for very high or very low intelligence seem to lower fitness. Selection for intelligence in England to-day seems to be partly evolutionary, making for a slight lowering of intellectual capacity, and partly conservative. It must be emphasized that all selective trends of the second type may be rapidly altered by changes in the social or microbic environment.

Selection for heterozygosis has not been demonstrated in man, though it may exist for the *M* and *N* agglutinogens. If it exists it tends to preserve variability, but to check some possible evolutionary trends. Our main knowledge is of the fourth type of selection. Some abnormal genes, e.g. those for ichthyosis foetalis and the amaurotic idiocies, are lethal. Others, such as those for haemophilia, epiloia, and xeroderma pigmentosum, are sublethal. Still others, such as those for albinism and various types of imbecility, lower the fitness to a substantial but unknown extent.

The frequency of a lethal or sublethal genotype is equal to the mutation rate multiplied by a small factor, when equilibrium is reached. Dominants and sex-linked recessives are always near equilibrium, but owing to the recent relaxation of human inbreeding, autosomal recessives are far below their equilibrium frequency. Hence they are rarer in man than in most animals.

A given genotype may be considered desirable for four reasons. It may cause high fitness in its bearers. It may tend to increase their economic or social success, or their value to the community. It may promote the numerical increase of the community to which they belong. Or it may tend to make that community more valuable to the world. Genotypes which are desirable from one of these standpoints may be undesirable from another. Natural selection only favours genotypes of the first type directly, though it may possibly sometimes favour those of the third indirectly.

116

HALDANE, J.B.S. *New Data on Partial Sex-linkage in Man*

The human *X*- and *Y*-chromosomes appear to have a segment in common. If so, genes in this segment occasionally cross over in relation to the differential segments carrying the completely sex-linked genes. Women transmit partially sex-linked genes equally to both sexes. But a man who has got such a gene from his mother transmits it mainly to his daughters, whilst if he has got it from his father he transmits it mainly to his sons.

Three new pedigrees of dominant retinitis pigmentosa bring the total children of affected males up to 314 with 134 cross-overs. Thus $d=2{\cdot}54\sigma$. But if two pedigrees, in which the gene sometimes caused a condition diagnosed as optic atrophy, be omitted, we have 118 cross-overs out of 288, and $d=3{\cdot}01\sigma$. The evidence that this gene shows partial sex-linkage in some pedigrees is thus strengthened.

When cousins marry and produce recessive offspring, a partially sex-linked gene is likely to appear in the offspring of the same sex as the paternal grandparent through whom the parents are related. Burks has severely criticized my former data on this topic. Whilst I can accept much of her criticism, I think the evidence for partial sex-linkage in Usher's pedigrees of recessive retinitis pigmentosa without deafness remains unaffected.

Where the relationship between the parents is unknown we must use Fisher's "score"

$$u=(a-b-3c+3d)^2-(5a+b+9c+9d),$$

where a and b are the numbers of normal males and females, c and d of affected males and females. This has a positive expectation if there is partial sex-linkage.

In the absence of linkage the cumulants of the distribution of u are

$$K_1=U_1\ K_2=2\ [(S_1+9S_2)^2-(S_1+81S_2)],$$
$$K_3=8\ [(S_1+9S_2)^3-3\ (S_1+9S_2)\ (S_1+81S_2)+2\ (S_1+729S_2)],\ \text{etc.},$$

where S_1 and S_2 are the numbers of normal and affected sibs. As a test of significance a comparison of u with $K_2^{\frac{1}{2}}$ is rather misleading, since K_3 and K_4 are both positive, and may be large. Hence a positive value of u equal to three times its standard error may not be very significant.

Using a transformation of u given by the author elsewhere, we can make its distribution nearly normal, and then find that the probabilities of obtaining the values of u which suggest partial sex-linkage of four recessive genes remain below 0·01 in each case. The general result is that the hypothesis of partial sex-linkage has not been disproved, and the evidence for it has been slightly strengthened in some cases and weakened in others.

117

HALL, Sir A. DANIEL. *How does the Plant Breeder go to Work?*

A collector sends home a packet of seeds of some desirable plant not hitherto in cultivation; it is a commonplace experience that for some years the plants are all alike, then new forms appear, rare at first but in increasing variety as intercrossing proceeds. Darwin, following T. A. Knight, considered that rich soil, etc., supplied a stimulus to variation. Nowadays we recognize that a species in nature is a mixed population containing many latent recessives. In cultivation, when all the seedlings are brought to maturity, chance fertilization brings about the appearance as phenotypes of these recessives, which are immediately perceived and perpetuated. As cultivation proceeds on a large scale new mutations occur, and if of any commercial value are selected and bred up. Illustrations from the history of the Chinese *Primula* within the last hundred years. The rate of mutation may be increased. Other quantitative characters like size, sugar content, habit of growth, may be controlled by multiple factors so that in practice improvement appears to proceed on Darwinian lines by the accumulation of infinitesimal advances.

When hybridization is possible the plant breeder has more genes to work with. New characters may be created. Illustration from the changes in anthocyanin pigments of *Streptocarpus* following hybridization.

Very commonly hybrids are sterile. Sterility may

be eliminated if a tetraploid can be obtained from the hybrid. *Primula kewensis*, *Digitalis mertonensis* (*purpurea* × *ambigua*), *Aesculus carnea* (pink horse-chestnut). Polyploidy by somatic doubling. Tetraploids in nature—*Tulipa silvestris*. Gigantism—*Campanula persicifolia* "Telham Beauty", etc. Methods of inducing polyploidy. Sexual production of polyploids, usually triploids. Triploids by union of diploids and tetraploids. Accidental production of tetraploids—blackberry "John Innes". *Delphinium Ruysii*. Complex polyploids—dahlia, plum, loganberry. Secondary polyploids—apple. Graded inheritance consequent upon repetition of genes.

WHAT CAN GENETIC SCIENCE DO FOR THE PLANT BREEDER?

Warning off. Line breeding against mass selection in fixing a type. Heterozygous characters cannot be fixed. Seed production to take advantage of hybrid vigour. Calculation of odds against desired combination. Chimaeras result in apparent anomalies. Aneuploids usually of low viability but occasional possibilities of exceptional results. Danger of exclusive breeding for particular characters, return to wild types—strawberry, sugar cane, potato.

Science of least value with plants possessing a long history—rose, iris, tulip, wheat. The value of big battalions. Element of chance still dominant, outstanding happenings reflect the infinite number of trials made in nature.

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HARLAND, S.C. ***Genetical Studies in the Genus* Gossypium *and their Relationship to Evolutionary and Taxonomic Problems***

I do not know how many of this audience are believers in the Darwinian theory of natural selection as the main explanation of the origin of generic and specific differences in living organisms. For at the time of the last Genetical Congress in 1932 the number of geneticists who would have subscribed whole-heartedly to this theory was relatively small. It is not difficult to think of reasons for non-adherence. The hereditary variations upon which studies had been conducted for many years after the rediscovery of Mendel's work possessed usually the relationship of dominant and recessive, or at any rate exhibited clear-cut segregation, and neither dominant nor recessive phases of single genes seemed to provide the kind of variation which natural selection could make use of for evolutionary purposes. To-day I imagine the majority of geneticists would subscribe to the thesis that the main cause of evolution has been gene substitution on a background of cytological events.

Probably the attainment of this view was retarded by the original studies of Mendel himself. Mendel found clear-cut segregation in a number of pairs of characters in *Pisum sativum*. From 1900 onwards every geneticist tried to find in his material examples of the same type of segregation, and material which did not conform was regarded as unsatisfactory or unsuitable. I have even heard genes described as "bad" genes because they did not conduct themselves properly, nor segregate nicely.

The plant used by Mendel was *P. sativum*, an ancient domesticated species, and he investigated the clearly demarcated differences which had doubtless originated by mutation, and which had been preserved by human agency. The rest of the genotype provided a relatively constant and stable background upon which both the dominant and recessive phases of his genes were clearly distinguishable. If, however, he had been unfortunate enough to work with an interspecific hybrid in which the constituent species possessed innumerable differences in minor genes, that is, possessed widely divergent genetical backgrounds, a given pair of characters would have manifested themselves upon an enormously complicated series of new backgrounds and he would have got typical cases of blending inheritance instead of clear-cut segregation.

Now that we know that blending inheritance is explainable by the fact that segregation is taking place in genetical backgrounds with or without a pair of "main", "major", or "key" genes—according to which term is proposed—and as we also know that blending inheritance is the rule in most species of hybrids, attention has now been transferred from the so-called "good" genes to the so-called "bad" genes. Consequently the study of species differences now largely resolves itself into a study of genetical backgrounds or modifier complexes, and how they are built up—in short, the study of the genetical architecture of the species.

It is perhaps necessary at this point to define a modifier complex as an assemblage of genes which conjointly affects the degree of expression of a given pair of alleles. I shall also put forward the hypothesis that it is a huge interlocking series of modifier complexes that characteristically marks off one species from another in a given genus. If this hypothesis is tenable it should be possible to convert cases of typical interspecific blending inheritance, due to segregation of modifiers, into simple cases of clear-cut monohybrid inheritance. Using as material species in the genus *Gossypium*, it has been abundantly demonstrated that this can be done by a sufficient number of backcrosses of given heterozygotes to either or both of the parental species, thus standardizing the genetical background. The transference of genes from

one species to another or, in other words, from one background to another by repeated backcrossing has proved to be a powerful method of obtaining knowledge about the genetical architecture of the different species of the genus *Gossypium*.

In order to investigate the comparative genetics of a group of species in a genus, certain prerequisites are necessary. First the species should be good species, recognized as such by competent taxonomists; second, they should differ in a large number of characters; third, although some sterility is permissible it should not be extensive enough to preclude genetical analysis; fourth, gross cytological abnormalities should not intervene; and fifth, the species chosen for experiment should if possible have been separated geographically for a long period of time. The genus *Gossypium* provides material admirably fulfilling these criteria of suitability for interspecific genetical analysis. The genus is divided into an $n=13$ chromosome group and an $n=26$ chromosome group of species, with great diversity of characters. The 13-chromosome group contains at least eleven wild species from Asia, Africa, Australia, North America, and the Galapagos Islands. The 26-chromosome group comprises six well-marked wild and cultivated species confined to the American continent and certain Pacific Islands. It has been established cytologically by Skovsted and Webber that the $n=26$ chromosome American species are amphidiploids containing two 13-chromosome genoms, of Asiatic and American origin respectively. Further, genetical studies of the relationship of the amphidiploids to their presumed diploid components have thrown much light on the evolutionary history of the former, and since evolutionary questions are included within the scope of this paper, the facts may be discussed at some length.

Evolutionary history of the new world amphidiploid group

The cytological conclusions were confirmed by genetical evidence. A series of multiple alleles controlling anthocyanin pigmentation of plant body and base of corolla (petal spot) exists in the New World amphidiploids. There are at least seven alleles in the group, and to these we were able to add another. A gene for red plant body in *G. arboreum* (Asiatic), with $n=13$ chromosomes, was transferred to amphidiploid *hirsutum* by repeated backcrossing. This new member of the multiple allele series for anthocyanin was called $\mathbf{R^A}$, and manifested itself on the two different species backgrounds as follows:

arboreum background—red plant body, red flower, large and intense petal spot.
hirsutum background—dilute red plant body, flower flushed red at edges, no petal spot.

To complete this section of the story a list of the best known alleles at this locus may be given:

$\mathbf{R^B}$—red plant body, no petal spot[1] (*G. barbadense* L.).
$\mathbf{R^P}$—red plant body, no petal spot[1] (*G. purpurascens* Poir).
$\mathbf{S^B}$—[2]green plant body, strong petal spot (*G. barbadense* L.).
$\mathbf{S^P}$—[2]green plant body, strong petal spot (*G. purpurascens* Poir).
$\mathbf{S^D}$—[2]green plant body, strong petal spot (*G. Darwinii* Watt).
s—[2]green plant body, petal spotless[1] (*G. hirsutum*, *G. purpurascens*, *G. barbadense*).
$\mathbf{S^H}$—[2]green plant body, strong petal spot (*G. hirsutum* L.).

An entirely different duplicate gene for red plant body exists in *hirsutum*, the gene $\mathbf{R^H}$. The two $n=13$ Mexican species, *G. aridum* and *G. Armourianum*, both possess large petal spots. By repeated backcrossing it was found possible to transfer these two anthocyanin genes to a *hirsutum* background. The two genes concerned, $\mathbf{S^{ARM}}$ (petal spot of *Armourianum*) and $\mathbf{S^{ARI}}$ (petal spot of *aridum*), both proved to be at the same locus as $\mathbf{R^H}$, and we now had a new multiple allele series of four members:

$\mathbf{R^H}$—red plant body, no petal spot (*G. hirsutum* L.).
$\mathbf{S^{ARM}}$—green plant body, strong petal spot (*G. Armourianum* Kear).
$\mathbf{S^{ARI}}$—green plant body, strong petal spot (*G. aridum* Rose and Stand) Skov.
s—green plant body, no petal spot (*G. hirsutum* L.).

The fact that genes from both Indian and Mexican diploids can be inserted into New World amphidiploids, and can be assigned to known loci, completes the proof of the origin of the New World tetraploids. Since this group also has endemic members in the Pacific Fiji, Hawaii, Galapagos, etc., there is strong reason for supposing that the original amphidiploids date from a period when a land connexion existed from western America across the Pacific to the Dutch East Indies, and that they arose, possibly more than once, and from more than one combination of diploid species, at some point probably between Fiji and the Dutch East Indies in a now sunken landmass. Amphidiploid representatives survive in isolated and widely separated Pacific regions where

[1] "No petal spot" is a relative term. In *hirsutum* most types are completely devoid of anthocyanin colour, but some types possess one or two pigmented cells in the spot region. In *barbadense*, spotless may attain the grade of weak spotting, while *purpurascens* resembles *hirsutum*.
[2] Stem may be tinged in these types.

they have been left marooned. The Mexican diploids seem to be part of a relict Upper Cretaceous flora, and the Pacific amphidiploids must necessarily date from a time earlier than the isolation of Fiji, Hawaii, and Galapagos. The original amphidiploids, ancestors to the present Upland and Egyptian cottons, were thus synthesized in late Cretaceous or early Tertiary times, twenty to fifty millions of years ago.

A sidelight of some importance is that a resynthesis of the New World amphidiploid, which may for convenience be termed the tetraploid group, has recently been made by treating with Colchicine a hybrid between Mexican *G. Thurberi* and Asiatic *G. arboreum*. The untreated hybrid was completely sterile on both male and female sides, but while the new amphidiploid was male-sterile, it was completely fertile on the female side when crossed with commercial American or Egyptian cotton.

To sum up this section: It has been shown by a combination of genetical and cytological methods that the evolutionary history of the cultivated cottons can be traced back for several millions of years. At the present stage of our knowledge, mapping evolutionary history is analogous to the efforts of the early cartographers. They were almost invariably wrong about islands, and quite frequently they were also wrong about the size and position of continents, but their maps did provide a good foundation for further extension, alteration, or amplification.

Genic effects of long isolation

One of the chief objects of study was to give some kind of provisional answer to the question—What happens to genes and the characters in which they manifest themselves as a consequence of long-continued isolation? Crosses between *G. hirsutum* and *G. barbadense* have been studied in some detail, though a good deal is also known about crosses involving other New World species. *G. hirsutum* L. is the ordinary American Upland of commerce, while *G. barbadense* L. is the large Peruvian group including commercial Sea Island, Egyptian and Peruvian. Following Vavilov, the centres of origin of these two species are southern Mexico and the Andean region respectively. They have undoubtedly been separated for a long period of time. Several pairs of homologous characters occur in both *barbadense* and *hirsutum*. Examples are:

Petal spot—no petal spot,
Yellow corolla—cream corolla,
Yellow pollen—cream pollen.

Now when the inheritance of these characters is studied within the species, as in the cross *barbadense* petal spot × *barbadense* spotless, the results are reasonably free from complications and exhibit the usual type of monohybrid inheritance. It is only when we cross the *dominant* of one species with the *recessive* of the other that we encounter difficulties. Here the F_2 generally exhibits a series of minute gradations in the manifestation of the character, rendering classification impossible, and obscuring completely the boundaries of the three phases of the gene, AA, Aa, and aa. Referring especially to the character Petal Spot the following main facts were established:

(1) Spotted *barbadense* × spotless *hirsutum* gives a blended series in F_2.

(2) Spotted *hirsutum* × (relatively) spotless *barbadense* also gives a blended series in F_2.

(3) Spotted *barbadense* × (relatively) spotless *barbadense* gives 3 spotted : 1 spotless in F_2 (S^B–s^B).

(4) Spotted *hirsutum* × spotless *hirsutum* gives 3 spotted : 1 spotless in F_2 (S^H–s^H).

(5) Transference of *barbadense* spot (S^B) to *hirsutum* s, by repeated backcrossing, results in a new and extremely weak type of spot, i.e. spot almost vanishes.

(6) Transference of *hirsutum* spot (S^H) to *barbadense* s, by repeated backcrossing, results in a larger and more intense type of spot than S^B.

The first generalization of importance is that the genes for spot (using this phrase in the popular sense) are not *identical* in these two species. It can, however, be shown that they are both alleles at the anthocyanin (R^B) locus.

It follows that we have two different methods of constructing this character in the two species, viz.

(1) *barbadense*: Spot is constructed by using a "major" or "key" gene which by itself can produce little effect (e.g. when on *hirsutum*). To produce a fully developed, characteristic petal spot in *barbadense* the "key" gene, S^B, requires a series of plus modifiers to augment its effect.

(2) *hirsutum*: Spot is constructed by using a strong or potent "key" gene, with few or no plus modifiers.

A corollary to the first generalization is that if a character is built up by a strong key gene with few modifiers, the corresponding recessive is weakened in phenotypic expression, since the modifiers which as a group do have some effect in absence of the key gene are lacking. Thus "spotless" in *hirsutum* is usually completely spotless while the recessive phase in *barbadense* is weakly but definitely spotted, exhibiting the spot modifier complex acting alone, but in the same direction as the key gene. To sum up: Strong key gene is associated with weakly developed recessive phase; weak key gene is associated with strongly developed recessive phase.

The second important generalization is that the genetical architecture of the character petal spot is widely different in the two species, and is conditioned by numerous genic differences, so that the blending

inheritance found in F_2 of the species hybrid is due to the key gene being manifested on a complicated series of new modifier complexes resulting from new associations of the modifier complexes of both species.

Genes for petal spot have also been transferred from other species to either a *hirsutum* or *barbadense* background, e.g. from *G. purpurascens*, *G. Darwinii*, *G. arboreum* ($n=13$), *G. aridum* ($n=13$) and *G. Armourianum* ($n=13$).

A. *G. purpurascens* ($n=26$). Transference of petal spot from *purpurascens* to *hirsutum* resulted in some weakening of the petal spot, but complete transference was not possible owing to the fact that the spot gene S^P became unstable on a *hirsutum* background, mutating to the recessive spotless so frequently that it could not be retained.

B. *G. Darwinii* ($n=26$). Similar results were obtained with *Darwinii* when transference of spot to *hirsutum* was attempted.

C. *G. arboreum* ($n=13$), Asiatic diploid. As has been previously noted, the strong colour complex—red flower, strong spot, red plant body—of *arboreum* became greatly diluted in intensity on a *hirsutum* background. The red plant body became a weak red; the red flower had the coloration reduced to a red flush on the petal edges, and *the petal spot disappeared entirely*.

We have then in *arboreum* a third method of constructing petal spot.

(3) *Arboreum* petal spot is constructed by using a series of modifiers, there being no key gene in the spot complex transferable to *hirsutum*.

D. *G. aridum* ($n=13$), Mexican diploid. On a *hirsutum* background the *aridum* spot became fractionated and also became mutable. Evidently it is a weak key gene, probably accompanied by a strong modifier complex as in *barbadense*.

On a *barbadense* background, *aridum* spot was large and intense, and not mutable.

E. *G. Armourianum* ($n=13$), Mexican diploid. On a *hirsutum* background the *Armourianum* spot increased in size and intensity, and was not mutable. It is a strong key gene of the *hirsutum* type. The recessive is known in nature and is also of the *hirsutum* type, being weakly developed. On a *barbadense* background the spot became very large and intense and it seems, therefore, that some of the genes in the plus modifier complex of *barbadense* can act also as plus modifiers of both *aridum* spot and *Armourianum* spot.

Here, then, in the species *hirsutum*, *barbadense*, *purpurascens*, *arboreum*, *aridum*, and *Armourianum*, there are as many different ways of constructing petal spot as there are species. No doubt if we could study the petal spots of other species and of closely allied genera such as *Thespesia*, *Cienfuegosia*, *Gossypioides*, *Kokia*, etc., we should encounter still further types of construction.

Thus the first genetical effect of geographical isolation is that homologous characters become built up in different ways, and broadly speaking there are three main types of construction:

Type 1. A strong key gene with few or no modifiers (e.g. *hirsutum* spot).

Type 2. A weak key gene accompanied by plus modifiers (e.g. *barbadense* spot).

Type 3. An association of modifiers with no key gene (e.g. *arboreum* spot).

I am led to believe that the distinction between these three is of great evolutionary significance. It is manifest that a character such as petal spot must have some definite import to the species, for otherwise it is difficult to put forward reasons for its existence in such a variety of genetical forms. Nevertheless, in the principal commercial cotton of the world, *hirsutum*, petal spot is in general absent, the spot gene being found only in a few rare varieties. Assuming, however, that the character petal spot is of importance, it is obvious that the adoption of type 1 by the species might be disastrous, since mutation to recessive of the powerful key gene would result in the disappearance of the character. That is, in type 1 the integrity of the character depends on the fact that one gene is able to perform the functions of a great many. On the other hand, mutation of a weak key gene to recessive still leaves the plus modifier complex manifesting itself as a weak spot, but nevertheless capable of reinforcement by the drifting in of further plus modifiers. That this is possible is shown by the fact that the second generation of a cross between *hirsutum* spotless and *barbadense* spotless contains new recombinations of modifiers with petal spots as large as those of typical *barbadense*. Here we have constructed new petal spots of type 3. *Hirsutum*, although spotless, evidently contains modifiers capable of acting as plus modifiers of the modifiers of *barbadense*.

Type 3 would seem on the face of things the safest and most stable method of character construction, since if mutation takes place in some loci the character is capable of repair by accumulation of new modifiers.

Adopting analogies from the realm of human affairs, we may describe the principles involved in the three methods of construction as autocratic, democratic and anarchic respectively. The evolutionary history of a simple plant character may well have a deep significance for the sociologist.

It may be a point of criticism that the generalizations arrived at by a study of the character petal spot are not applicable to characters in general, so I shall next deal with some experiments on the behaviour in interspecific crosses of the mutant type known as Crinkled Dwarf. The results are of importance not

only for the evaluation of current theories of dominance but also for estimating the degree of taxonomic divergence between species in the genus *Gossypium*.

The Crinkled Dwarf mutant occurs rather commonly in commercial fields of *barbadense*, and in this species dominance of normal over mutant is complete. Hutchinson and Ghose have recently found the mutant also in *hirsutum*, but it is exceedingly rare. Crosses between the normal of one species and the crinkled of the other give an F_2 characterized by typical blending, embracing a minutely graded series of forms ranging from an almost lethal, greatly exaggerated crinkled (super-crinkled) to a phenotypically normal type exhibiting no trace of crinkled (pseudo-normal). It is possible to transfer *barbadense* crinkled to a *hirsutum* background, and when so transferred it behaves as a typical recessive. The F_1 of *barbadense* crinkled by *hirsutum* normal is not normal, however, but intermediate. Likewise when *hirsutum* normal is transferred to the background of *barbadense* the F_1 is again not normal but intermediate. Time to develop the whole of the argument is lacking, so that quite briefly we may add a further generalization to those already put forward, and state that in passing from one species to another a different method of producing dominance is encountered. *Barbadense* produces dominance to crinkled by using a normal allele of great dominance potency on a (within the species) relatively fixed and not easily modified background, while *hirsutum* does it by using a weak normal allele with a series of plus, reinforcing modifiers. That is, the *barbadense* normal allele performs a function which in *hirsutum* is performed by many alleles. *Barbadense* normal (in relation to crinkled) is thus of type 1, while *hirsutum* normal is type 2, and the pseudo-normal of the interspecific cross is type 3.

It has already been stated that a strong key gene implies a weakly developed recessive phase, whilst a weak key gene is associated with a strongly developed recessive phase. Applying this rule to the present case the *hirsutum* heterozygote could progress from intermediate to fully dominant by accumulation of plus modifiers which would *simultaneously improve* heterozygote and recessive, so that as the heterozygote approaches normality the recessive approaches intermediacy. This is actually the case. *Hirsutum* crinkled is a more improved (i.e. nearer normal) form than *barbadense* crinkled, and is capable of passing to complete normality by accumulation of further plus modifiers. By stringent selection new forms of *hirsutum* crinkled have been produced which are practically indistinguishable from normal. On the other hand, the potent normal allele of *barbadense*—able to produce complete dominance by itself—has rendered it unnecessary to improve the recessive crinkled, so that *barbadense* crinkled is not only phenotypically less improved than *hirsutum* crinkled, but shows also much less capacity for improvement.

Certain workers (Hutchinson and Ghose) have argued that the attainment of dominance to crinkled in the cultivated cottons is comparatively recent and is due to the conditions of domestication. That this view is incorrect is shown by the results of experiments in which crinkled was transferred to the background of a wild *G. purpurascens* (*Morilli*) from the west coast of Mexico. When so transferred, the extracted crinkled was a considerably improved form, similar in this respect to *hirsutum*, and normal was again completely dominant. Further experiments revealed that the normal allele of this type was of the weak *hirsutum* type.

It has also been found possible to transfer normal alleles of crinkled from the Mexican diploid species to a *barbadense* background, and the following main facts were established:

(1) The *Armourianum* allele was completely dominant, resembling the *barbadense* allele.

(2) The *Thurberi* allele was incompletely dominant, resembling the *hirsutum* allele.

It thus appears that the history of the origin of dominance at the crinkled locus of the New World amphidiploids extends backwards into Upper Cretaceous times to the Mexican genom. The Asiatic genom does not appear to possess a normal allele of crinkled.

Normal alleles at the crinkled locus are capable of being arranged into a series with graded dominance potency, and it seems that the number of such alleles must be rather large.

It will be recollected that the F_2 of *barbadense* crinkled by *hirsutum* crinkled give rise to a diverse series of crinkled forms ranging from semi-lethal (super-crinkled) to phenotypically normal (pseudo-normal). By self-fertilization for seven generations, several different grades of crinkled were isolated in an approximately homozygous condition. These were used as bases on which to transfer various normal alleles, though the experiments had unfortunately to be abandoned when they were beginning to give interesting results. The following points were established:

(1) The strong *barbadense* normal allele proved to be completely dominant on all grades of crinkled, including super-crinkled. But, although the heterozygote with super-crinkled was *phenotypically* normal it was a very weak type and would not have survived to produce offspring in field culture. The homozygous normal was also very weak, and would have survived in field culture with some difficulty. The survival value of homozygous normal (on super-crinkled back-

ground) was certainly *less* than that of the original crinkled *barbadense* mutant.

In regard to the behaviour of *barbadense* normal on other crinkled backgrounds, it may in general be said that improvement in the heterozygote accompanied improvement of the crinkled recessive base, i.e. the better the recessive base, the better the heterozygote and, though less certainly, the better the homozygous normal.

These experiments then, though incomplete, indicate that dominance is produced by a normal allele of great potency, on a very diverse series of crinkled backgrounds, though dominance can occur in types of low survival value. The modifying factors which simultaneously improve the phenotypic appearance and enhance the survival value of the crinkled (aa) phase also have similar effects on the Aa and AA phases. In field populations the survival value of normals is necessarily maintained by rigorous selection. High survival value of normals thus implies a modifier complex selected on its own account which conditions a certain survival level, and a correlated phenotypic expression in the recessive. This level, as it occurs in any wild or cultivated cotton known, is certainly one that would not permit a recessive of so low a survival value as the extracted super-crinkled. It can, then, be said that should crinkled occur as a completely new mutation, it will necessarily be relatively efficient. The first stage in the improvement of crinkled, then, is due to modifiers preserved as being of value to conserve the fitness of the Normal. Other fitness modifiers may have been accumulated by the recessive, or heterozygote, as a result of direct selection pressure, and transferred to the Aa or AA phases as the case may be, by natural crossing. Improving modifiers of the Aa or aa phases would probably have only a neutral effect on the AA phase, since the latter has already made all the improvement possible by direct selection pressure. The improving modifiers would, however, tend to push both heterozygote and recessive towards the fitness level of the homozygote AA.

(2) Transference of *hirsutum* normal to the graded series of crinkled backgrounds.

On a super-crinkled background the Aa phase was very crinkled and very weak, more so than the original crinkled mutant. It could not possibly survive under natural conditions, nor could even the AA phase. It follows then that the mutant in *hirsutum* must *ab initio* have been at rather a high level, and much better than super-crinkled, in order to correspond with a superior normal.

Comparing the progress of recessive towards normal in *barbadense* and in *hirsutum*, it may be argued that such progress is slower when the normal allele is of great potency (*barbadense*) than when it is weak (*hirsutum*). The heterozygous *barbadense* being already phenotypically dominant can only assist the recessive to improve in so far as the additional fitness modifiers which it accumulates affect the phenotypic manifestation of the recessive. The heterozygous *hirsutum*, on the other hand, may have appeared as an intermediate, and in the process of attaining dominance by accumulation of modifiers, could at the same time assist the recessive in its progress towards normality. In a normally partially cross-fertilized species such as cotton where intertransference of modifiers from Aa to AA and thence to aa is not infrequent this process could be expedited.

Taxonomic classification and genetics

So far I have dealt in a necessarily discursive way with experiments which throw some light on evolutionary questions in the genus *Gossypium*. The main conclusion may be summed up, namely, that species differences have been shown to involve differences in genetical architecture, including not only differences in the way characters are built up, but also different dominance mechanisms. The value of genetical studies for the elucidation of taxonomical relationships need not, therefore, be further stressed. It is clearly evident that without genetical and cytological data it would not even be possible correctly to delimit the boundaries of the genus *Gossypium*. It is a matter of more than casual interest to record that although the earlier taxonomists were badly wrong on many occasions, it is nevertheless surprising how often they were right. Sometimes, as in the case of *G. Kirkii*, they classified species as a *Gossypium*, which on cytological grounds and grafting relationships must be put in another genus, and on two occasions species known now to belong to the genus on good cytological and genetical grounds were actually assigned to different genera. The wild cotton of Arizona, formerly called *Thurberia thespesioides* A. Gray, is now a member of the genus *Gossypium* under the name *G. Thurberi* Tod, while *Erioxylum aridum*, Rose and Standley, is now *G. aridum* Rose and Standley (Skovsted). *Thurberi* and *aridum* are both North American species with 13 chromosomes, and are descendants of the primitive species which formed one of the components of the ancestors of the present New World amphidiploid group.

Finally, it may be emphasized that the results obtained from *Gossypium* studies are not to be universally applied to other genera. In *Gossypium* we are dealing with a genus in which geographical isolation has played a large part in the formation of species, and as is well appreciated, the term species changes its significance from the point of view of genetical architecture according to the genus.

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HARTMANN, M. *Das Wesen und die stofflichen Grundlagen der Sexualität*

Die Untersuchungen der letzten 30–35 Jahre über Geschlecht und Geschlechtsbestimmung bei Tieren und Pflanzen haben es ermöglicht, eine allgemeine Theorie der Sexualität aufzustellen, die sich in folgende 3 Thesen zusammenfassen lässt: (1) Bei allen Organismen gibt es zwei *bipolar verschiedene Geschlechter* mit Ausbildung weiblicher und männlicher Geschlechtszellen, auch dort wo äusserlich keine Unterschiede zwischen diesen beiden Geschlechtern und Geschlechtszellen vorhanden sind (*bipolare Zweigeschlechtlichkeit*). (2) Jedes Geschlecht und jede Geschlechtszelle enthält zugleich die Fähigkeit zur Ausbildung des entgegengesetzten Geschlechts (*bisexuelle Potenz*). (3) Die Geschlechtsbestimmung erfolgt durch *die relativ verschiedene Stärke* äusserer oder innerer modifikatorischer oder erblicher, genetischer Faktoren.

Das Vorhandensein zweier bipolar verschiedener Geschlechter ist bei den Metazoen, höheren Pflanzen und den meisten Protisten und Thallophyten eine einfache Tatsache. Bei den isogamen Protisten und Thallophyten sind vielfach durch Züchtungs- und Kombinationsversuche zwei erblich getrenntgeschlechtliche Sorten von äusserlich gleichen Organismen und Gameten (♂ und ♀) nachgewiesen worden (haploide genetische Getrenntgeschlechtlichkeit). Ausserdem konnte für diese genetisch getrenntgeschlechtlichen wie für die gemischtgeschlechtlichen Protisten ohne erbliche Geschlechtsbestimmung das Vorhandensein zweier verschiedener (♂ und ♀) Sexualstoffe festgestellt werden.

Die (2) allgemeine Gesetzmässigkeit, die allgemeine bisexuelle Potenz jedes der beiden Geschlechter, ist von Correns schon bei den ersten Versuchen über die Vererbung des Geschlechts bei Pflanzen aufgezeigt worden, und trat bei Tieren durch die Versuche von Goldschmidt an den Erscheinungen der Intersexualität bei der Kreuzung geographisch verschiedener Rassen von Schmetterlingen besonders eindrucksvoll zutage. Dasselbe zeigten die triploiden intersexen Mutanten und Bastarde von *Drosophila* (Bridges) und von Schmetterlingen. Die beiden letzterwähnten Versuchsreihen (an Intersexen) ergaben zugleich, dass die erbliche Geschlechtsbestimmung der Tiere durch die relativ verschiedene Stärke ♂ und ♀ Geschlechtsrealisatoren zustande kommt (Goldschmidt, Bridges).

Bei haploiden Protisten und Thallophyten wird die bisexuelle Potenz der ♂ und ♀ Gameten und die relative verschiedene Stärke modifikatorischer oder genetischer Faktoren (Realisatoren) am eindringlichsten durch die Erscheinungen der sog. relativen Sexualität bewiesen. Die relative Sexualität tritt zutage bei der Kombination der Gameten von Rassen oder Modifikationen von verschiedener sexueller Stärke, indem sich z. B. eine weibliche Gametensorte A gegenüber einer männlichen Gametensorte B als weiblich, gegenüber einer stärker weiblichen Gametensorte C jedoch als männlich erweist.

Im letzten Jahre haben Kuhn und Moewus für den einzelligen pflanzlichen Protisten *Chlamydomonas eugametos* f. *simplex* die chemische Struktur dieser Sexualstoffe aufklären können. Der weibliche wie der männliche Stoff wird aus der gleichen labilen Vorstufe V in blauem und violettem Licht gebildet und geht schliesslich in eine unwirksame Endstufe Ko über. Der weibliche Stoff besteht aus einer Mischung von 3 Teilen V and 1 Teil Ko, der männliche umgekehrt aus 1 Teil V und 3 Teilen Ko. Die Vorstufe V und die Endstufe Ko stellen nur verschiedene Zustände desselben chemischen Stoffes, eines *Carotinoids* dar. Die Vorstufe V hat sich als *Cis-Crocetindimethylester*, die Endstufe Ko als *Trans-Crocetindimethylester* nachweisen lassen.

Von dieser Grundlage aus gelang Moewus nun auch die Aufklärung der *relativen Sexualität*. Innerhalb der *Chlamydomonas eugametos*-Gruppe waren vier Rassen, resp. Arten von sexuell verschiedener Stärke aufgefunden worden, bei denen relative Sexualität vorkommt. Die verschiedenen starken weiblichen und männlichen Gameten unterscheiden sich durch den verschiedenen Anteil von *Cis-* und *Trans*-Crocetindimethylester. So ist das Verhältnis von *Cis-* zu *Trans*-Ester bei der stärksten weiblichen Art ($♀^4$) $95^{cis}/5^{trans}$, bei der stärksten männlichen ($♂^4$) $5^{cis}/95^{trans}$, bei der schwächsten weiblichen ($♀^1$) $65^{cis}/35^{trans}$ und bei der schwächsten männlichen ($♂^1$) von $35^{cis}/65^{trans}$. Ist der *Cis-Trans*-Unterschied grösser als 20, so findet Kopulation zwischen gleichgeschlechtlichen Gameten statt (relative Sexualität). Die drei eingangs hervorgehobenen Grundlagen einer allgemeinen Sexualitätstheorie, die bipolare Zweigeschlechtlichkeit, die bisexuelle Potenz und die relative Stärke der Geschlechtsbestimmung (relative Sexualität) finden demnach bei den untersuchten *Chlamydomonas*-Arten resp. Rassen ihre rein stoffliche Erklärung, indem sie auf das verschiedene Mischungsverhältnis der *Cis-Trans*-Carotinoide zurückgeführt werden.

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HAYS, F.A. *Inheritance of Comb Type and Ear-lobe Colour in Rhode Island Reds*

This study included 560 single-comb Rhode Island Red cockerels and pullets hatched in four successive years at the Massachusetts Agricultural Experiment

Station. All birds were classified for comb type and ear-lobe colour at six months of age.

Comb types studied were normal, and wavy and lopped condition of the comb were variations in the same character. The data indicated that two dominant complementary autosomal genes were responsible for the lopped or wavy comb condition. There was evidence of partial sex-limited inheritance but no evidence of sex-linkage.

Ear-lobe colours considered were normal red and red and white mottled. A considerable range occurred in the amount of white in the ear lobes, but no attempt was made to class these quantitatively. The data available indicated that the mottled ear-lobe condition was produced by two dominant complementary autosomal genes. There was no evidence of sex-linked inheritance, but the data showed partial sex-limited inheritance of the mottling character.

The complex nature of the two characters studied made linkage determinations impossible with the present stock.

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HEITZ, E. ***The Relationship between the Nucleus and Chromosome Structure and Gene***

The demonstration of the connexion between heterochromatin and the chromocentres led to the understanding of the structure and mechanism of the salivary gland chromosomes, and this in turn revealed the nature and importance of the inert regions of the chromosomes as well as the correspondence between genes and chromomeres, and the demonstration of the position effect. Work on the same lines has revealed the existence of endomitosis and the somatic reduction of polyploid nuclei.

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HENDERSON, D.K. ***Eugenics and Insanity***

In the past, the general outlook regarding the relationship of eugenics to insanity has been much too circumscribed; arguments are advanced showing the importance and necessity of effecting an alteration. Eugenics must embrace euthenics, while insanity must be broadened so as to take cognizance of every departure from mental or nervous health, whether or not involving commitment to a mental hospital. It is maintained that eugenic prognosis must be based on the broadest possible biological, sociological, and environmental aspects. The various clinical groups exhibiting conduct disorder are enumerated and discussed, fatalistic views regarding predetermination are discountenanced, and the necessity for better medical education is emphasized. The specific issues of the negative and positive eugenic programmes are examined, and reasons are submitted suggesting that the sterilization laws at present in force in various countries can only have a limited individual significance, and, racially, are of no great importance.

The above discussion is applied to those specific types of mental disorder in which hereditary involvement is acknowledged, e.g. manic-depressive and schizophrenic states. The view is maintained that the best type of eugenic programme must be essentially educational, and that everything should be done to encourage a sense of individual and national prestige whereby the strength and virility of the people can be maintained. The positive constructive aspects of such a policy are emphasized.

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HERTWIG, PAULA. ***Erbänderungen bei Maüsen nach Röntgenbestrahlung***

Mäusemännchen wurden mit Dosen von 200–1600 r. bestrahlt. Bei jeder Dosis konnte in den ersten Wochen nach der Bestrahlung eine fehlergesicherte Herabsetzung der Fertilität festgestellt werden. Es gelang durch genaue Untersuchung der Ursachen der Fertilitätsherabsetzung (Spermamangel, Absterbehäufigkeit der Zygoten), sowie durch Beobachtungen der F_1 Tiere (Frühprobanden) festzustellen: (1) dass die spermiogenetischen Endstadien und die Spermatozyten strahlenempfindlicher sind als die fertigen Spermatozoen. (2) Dass die Zygoten vorwiegend auf frühen Furchungsstadien zu Grunde gehen, weil durch die Spermabestrahlung im männlichen Genom zahlreiche Chromosomenbrüche entstanden sind, deren Häufigkeit sich an dem Vorhandensein von überzähligen Mikrokernen (Bild) abschätzen lässt. Die Zahl der Mikrokerne steigt proportional der Bestrahlungsdosis (Tabelle).

Nach 600 r. und höheren Dosen, tritt nach Verbrauch der gespeicherten Spermatozoen eine Periode der temporären Sterilität ein. Die nach der Sterilitätsperiode gezeugten Würfe sind normal gross. Hieraus wird gefolgert, dass in den bestrahlten Spermatogonien (ruhende Kerne) entweder weniger Chromosomenbrüche entstanden sind, oder dass Zellen mit Brüchen während der Spermiogenese ausgemerzt werden. Weitere Unterschiede zwischen Früh- und Spätprobanden sind auffällig: Die Frühprobanden entwickeln sich schlechter (hohe Sterblichkeit), wir finden viele schlecht fertile und auch sterile ♂♂ und ♀♀. Die Spätprobanden unterscheiden sich nicht von den Kontrollen. Besondere Aufmerksamkeit wurde der schlechten Fertilität geschenkt, da

sie sich als erblich erwies. Die Beobachtungen über den Erbgang (mehrere Sippen bis zur 7. Generation (Bild), die Absterbehäufigkeit der Zygoten (56 % bei 1635 Implantationen), die Gesetzmässigkeit von früh- und spätabsterbenden Zygoten (im Stamm 623 starben von 384 Implantationen, 101 als 7–8 Tage alte Embryonen, 283 auf dem Keimblasenstadium ab (Bild)), die stärkere Herabsetzung der Wurfgrösse bei Paarungen von zwei schlecht fertilen Partnern der gleichen Sippe als bei Fremdpaarungen (2,38 zu 3,28 bei 7,12 normaler Wurfgrösse), die Häufigkeit von schlecht fertilen Tieren in der Nachkommenschaft von schlecht fertilen (etwas mehr wie 50 %)), macht es so gut wie sicher, dass die Fertilitätsherabsetzung durch reciproke Translokationen bedingt ist, wie schon Snell zur Erklärung seiner Mäuseversuche annahm. Die Häufigkeit der herabgesetzten Fertilität ist recht hoch, nach 1000 r. sind nur noch circa 55 % der Frühprobanden gut fertil (Tabelle).

Die F_3 Generation nach Bestrahlung wurde auf rezessive letale und phänische Faktoren untersucht. Es gelang der Nachweis einer erhöhten Mutationshäufigkeit nach Bestrahlung. 36 Früh- und 82 Spätprobanden wurden durch markierte Rückkreuzungen und Sektionen geprüft. In der Nachkommenschaft der Frühprobanden wurden zwei kümmerwüchsige Mutanten und auf Grund von Wurfgrössenbeobachtungen und Sektionsergebnissen vier Letalfaktoren, von denen der eine mit den Farbgen d eng gekoppelt ist, gefunden. Unter den Spätprobanden-Nachkommen wurden drei phänische Mutanten gefunden (Zwergwuchs, Oligodaktylie, Anämie (Bilder)), alle drei nach 1500 r. Bestrahlung. Der weitere Nachweis von zwei Letalmutationen ist nicht ganz gesichert. Das Gen für Anämie (ev. verursacht durch hämolytischen Ikterus) ist mit dem Farbgen c eng gekoppelt.

Unter 72 ebenso geprüften Kontrollen wurde keine phänische Mutation, jedoch zwei Letalmutationen gefunden.

Eine vorläufige Auswertung der Versuche hinsichtlich der Mutationsrate bringt eine Übersichtstabelle.

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Hiorth, G. ***Versuche mit kultivierten und natürlichen Formen von Arten der*** **amoena-*Gruppe von*** **Godetia**

Die Versuche mit *Godetia* wurden im Jahre 1930 an Gartenrassen begonnen und 1936 durch Einsammlung von Samen aus zahlreichen natürlichen Lokalitäten erweitert.

Die kultivierten *Godetia*-Formen lassen sich in der Hauptsache zwei Arten zurechnen, *G. Whitneyi* und *G. amoena*. Letztere Art soll nach der neuesten systematischen Bearbeitung der Gattung (Hitchcock, 1930) an der Küste des Stillen Ozeans von Monterey (*ca.* 150 km. südlich von San Francisco) bis zur Südspitze der Vancouver-Insel in British Columbia vorkommen. *G. Whitneyi* dagegen soll nur an einer einzigen Lokalität, Shelter Cove, an der Küste des nördlichen Californiens gefunden sein.

Diese Anschauungen sind indessen durch die vorliegenden Untersuchungen nicht bestätigt worden. Im Jahre 1938 wurden zahlreiche F_1-Generationen zwischen natürlichen Rassen in Bezug auf ihre Pollenfertilität untersucht. Sämtliche benutzte Formen wurden bisher zu *G. amoena* gerechnet. Es zeigte sich jedoch, dass diese Rassen auf drei verschiedenen Arten zugeteilt werden müssen, deren Bastarde fast völlig steril sind. Vorläufig mögen diese Arten folgendermassen definiert werden:

I. Blütenknospen nickend *G. nutans*

II. Blütenknospen aufrecht
   a. Kronblätter in der Regel mit rotem Fleck. Dieser stets an der Basis des Kronblattes. Verbreitung: Südlich von Golden Gate (San Francisco) *G. amoena*
   b. Roter Fleck nie an der Basis, sondern in der Mitte des Kronblattes. Verbreitung: Golden Gate bis Vancouver-Insel, B.C. *G. Whitneyi*

Von diesen Arten scheint die stark variable *G. nutans* die grösste Verbreitung zu haben, indem sie viel weiter nach Osten vordringt als die beiden anderen Arten. Keine der Gartenrassen gehört zu *G. nutans*; obgleich Formen dieser Art sich gut als Zierpflanzen eignen dürften. Die Verbreitungsgebiete von *G. Whitneyi* und *G. amoena* scheinen scharf von einander getrennt zu sein, indem, soweit untersucht, alle Formen nördlich von Golden Gate sterile Bastarde mit den Formen südlich von Golden Gate ergeben.

Die genetischen Untersuchungen mit kultivierten Rassen, die sich hauptsächlich mit Formen von *G. Whitneyi* befassen, stiessen im Anfang auf grosse Schwierigkeiten, da die Gartenrassen in mancherlei Beziehung unbequem für Vererbungsversuche sind. Es gelang indessen im Laufe neunjähriger Versuche die meisten dieser Fehler auf dem Wege der Pflanzenveredlung zu eliminieren, so dass jetzt die Vorteile des Objektes stärker in den Vordergrund treten.

Da die *Godetia*-Rassen eine sehr grosse Variabilität in Blütenfärbung und -zeichnung zeigen, ist eine genetische Analyse dieser Eigenschaften hoffnungslos verwickelt, wenn nicht besondere Methoden angewandt werden. Es muss z.B. auf Grund langjähriger Erfahrung eine Standardrasse für Blütenfärbung

gewählt werden, und alle Typen, die nicht glatt gegen diesen Standard spalten, müssen kassiert werden.

Koppelungsuntersuchungen scheinen zu zeigen, dass die Mehrzahl der Koppelungen ziemlich stark sind. Eine Reihe geeigneter Merkmale für derartige Versuche steht zur Verfügung. Serien von multiplen Allelen für Blütenzeichnungen mit eigentümlichen Dominanzverhältnissen sind gefunden worden. Eine noch grössere Serie von Allelen für Blatt- und Kotyledonenzeichnungen wird untersucht.

Chromosomenmutationen sind häufig und recht auffällig in ihrer Erscheinung. Dagegen sind Genmutationen im allgemeinen selten, wenn auch einige Rassen eine stark erhöhte Mutationshäufigkeit zu haben scheinen.

Artbastarde innerhalb der *amoena*-Gruppe sind, wie erwähnt, hochgradig aber nicht absolut steril. *G. Whitneyi*, die sieben Paar kleine Chromosomen hat, lässt sich ferner mit der ziemlich entferntstehenden Art *G. Bottae* mit neun Paar grossen Chromosomen (nach Chittenden) kreuzen. Letztere Art enthält einige gute dominante Eigenschaften, die sich heterozygot, aber bisher nicht homozygot, in *G. Whitneyi* einlagern liessen.

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Hirschfeld, W.K. and Plank, G.M. v.d. ***Genetics and Animal Breeding***

Research work may be based on either a study of pedigree or deliberate experimentation, the latter being preferable, but limited, owing to its cost. The dangers of the pedigree method are outlined. Recent attention to the inheritance of productive characters has led to overlooking the inheritance of pathological ones. Must a family or group of high production value be sacrificed in order to throw out pathological hereditary aberrations? Test services of males with homozygous recessive defective females is recommended.

Resistance to disease is discussed. This probably exists but has not yet been proved for Dutch cattle in the case of tuberculosis. There are also genetic differences in the food requirements for different animals. In respect of the inheritance of productive characters, analysis is extremely difficult. The value of the progeny test is emphasized, but the analysis of breeding factors along the lines suggested by v. Patow is also of value and is an important method for the improvement of cattle. The use of such an hypothesis, though it may not be absolutely correct genetically, is of great practical benefit, but the adopted symbols should never be regarded as representing genes.

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Hoblyn, T.N. ***Testing New Varieties of Fruit Plants***

General problems in relation to testing of new varieties of plants grown for their fruit are discussed. It is noted that at the present day improvements are rather in the direction of fruit quality or resistance to disease than in actual yielding capacity. The preliminary test of a new group of individual seedling plants in which a proportion is eliminated on such grounds as season, colour, disease susceptibility, etc., needs no elaborate experimental design, though certain essential principles which should be remembered are suggested. The next stage involves the multiplication of the individual seedling plants, usually by vegetative propagation. During this period a further reduction in numbers should be effected on grounds of nursery performance. Propagation trials, in particular those of new varieties of rootstock, are discussed. Varieties not eliminated in these two preliminary tests, of which there may be quite a large number, are subjected to a more rigorous field trial. The principles which should govern the design of such large-scale variety trials are described with regard to:

(*a*) small fruits,
(*b*) tree fruits,
(*c*) rootstocks.

Suitable methods of experimental design are discussed, in relation to shape and size of plot, nature and distribution of controls, pollination, missing plants and border effects. Cultural problems in relation to such experiments are commented upon and the importance of efficient disease control, where the search for resistant varieties is not the primary object of the trial, is insisted upon.

Up to this point trials are probably confined to a single Station; improvements upon existing varieties grown under these conditions should now be submitted to a wider test under as many different conditions of soil and climate as possible. In this country the National Fruit trials, conducted by the Royal Horticultural Society, provide the necessary organization for this final test. The principles applicable to multiple trials of fruit plants are briefly discussed and certain essential requirements noted.

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Hogben, L.T. ***Genetic Variation and Human Intelligence***

The genetic basis of intelligent behaviour among human beings first became a focus of widespread scientific interest when Darwin's doctrine challenged

the Cartesian compromise which allocated the soul of man to philosophy and bequeathed his body to natural science. To-day we recognize that the genes which an individual receives determine what sort of neuromuscular organization it will develop in its usual conditions of growth. Certain features of neuromuscular organization are characteristic of the individuals of a species or of a genus, and as such depend on idiosyncrasies of what we now call the gene complex of such groups. Speaking broadly, two kinds of difference in the neuromuscular organization of different species may be distinguished. One includes differences in the character of relatively stable responses to external influences, as, for instance, whether bodily orientation is mainly determined by light or gravity, and, if by the latter, whether individuals positively or negatively *geotactic*. The other includes differences in the extent to which the pattern of behaviour is modifiable by previous experience, as, for instance, differences between the observed behaviour of sheep-dogs and snails. Pure lines of individuals, distinguished by their normal response to light or by their ability to learn how to thread a maze, have now been separated within the limits of a single species, and the genetic basis of certain defects of neuromuscular organization such as amaurotic family idiocy, juvenile amaurotic idiocy and Friedreich's Ataxia among human beings is well established. There is therefore no obstacle to the conclusion that interspecific behaviour differences have arisen by selective survival of mutations which turn up within the confines of a single species; and no modern biologist doubts that specific characteristics to which the word *intelligent* is usually applied when we are speaking of human beings have arisen in the same way.

In Darwin's time the study of inheritance and the study of behaviour had advanced little beyond the level of common sense, which was often plain nonsense. Studies on animal behaviour had been chiefly concerned with elucidating differences of the first type, and biologists were less alert to the difficulties of detecting genetic differences affecting the educability of animals. Galton, whose *Inquiry into Human Faculty* focused attention on the problem of the contribution of heredity to differences of human behaviour, showed himself to be aware of the difficulties when he wrote:

> Man is so educable an animal that it is difficult to distinguish between that part of his character which has been acquired through education and that which was in the original grain of his constitution.

The social background of the problem

Since these words were written the study of animal inheritance has become the most exact branch of biology, and the physiology of neuromuscular organization has expanded in all directions. That we cannot record equally noteworthy progress in the study of the genetic basis of human behaviour would therefore be surprising, if lack of effort or applied ingenuity were the only obstacles which impede the advance of scientific knowledge. On such an occasion as this it is fitting to examine such obstacles and to ask how they can be removed.

First among them we may recognize the way in which social preoccupations of one kind or another have deflected inquiry into unprofitable channels. The light-heartedness with which his followers shouldered the difficulties, which Galton himself recognized, is less perplexing when we consider the material and intellectual context in which the "eugenic movement" started. In the material context of the Darwinian controversy the geographical aspect of evolution was the predominating issue. Naturalists were specially interested in patterns of behaviour which distinguish animals living in different territories, and such differences are mainly dependent on the hereditary equipment characteristic of a species. Being at the same time preoccupied with defending the doctrine of human descent from an anthropoid stock, they were not encouraged to examine the credentials of analogous beliefsabout human beings. Contemporaneously the exploitation of peoples at retarded culture levels powerfully influenced the intellectual temper of a period which witnessed the abolition of negro slavery in America and an unprecedented, if unobtrusive, expansion of the British Empire.

In these circumstances the study of physical differences which distinguish different communities attained a popularity out of all proportion to the practical outcome, as we see it in retrospect. Since a large brain is a specific characteristic of human beings, it would not be surprising to find that interspecific differences of cranial capacity correspond with differences of intellectual accomplishment, and physical diagnosis might then provide an easy method of assessing the relative capability of individuals. The ascertained facts about what Pearson refers to as the correlation of "mind and body" are quite otherwise. In the words of Pearson himself they force us to conclude that "when we come to associate mental and bodily characters we find no correlation whatever of prognostic value". These words refer primarily to individual variation within a social group. There is also no certain relation between brain size or cranial capacity and the level of technological sophistication which different geographical varieties or communities of the human species have attained. The variations among races, nations and individuals are alike erratic. The cranial capacity of Leibniz, who discovered the calculus, wrote indifferently about philosophy, pro-

posed the first programme of co-ordinated philological research to promote a common language of world citizenship and managed the finances of a German state, was 1422 c.c., corresponding to a brain weight of 1257 g. The mean cranial capacities of Buriats, Kaffirs, south Germans, Eskimos and Tyrolese are respectively given by Martin as 1496, 1460, 1500, 1560 and 1359. Anthropometry may or may not be destined to advance medical prognosis in other directions. From our present standpoint there is little if any reason to encourage the further pursuit of physical anthropology in the hope that it will promote knowledge about the genetic basis of intelligent behaviour.

To many of Darwin's contemporaries natural selection was at once a sufficient justification for reviving the Calvinistic curse on the descendants of Ham and an alternative to Lamarckism as a plausible rationale for the inherent superiority of the newly enriched manufacturer and entrepreneur. The distaste of the latter for undertaking obligations accepted by an older aristocracy was reassured by such pronouncements as the ensuing passage from the writings of St George Mivart (1876), who defined natural selection as:

> ...a process which under bracing climates, rough living, and absence of medical aid is beneficial to a community however fatal to individuals by killing off weak members and reducing to a compact community of hardy and vigorous survivors.

By the end of the nineteenth century the demand for educational expansion sponsored in the early stages of industrialization by a social class, which was largely excluded from the older seats of English learning had become a challenge to their privileges as a new hereditary caste, and in Britain Galton's plea for "the study of those agencies under social control which may improve or impair the racial qualities of future generations" became a slogan for obstructing the general enlightenment of mankind. In Britain and in America eugenics has been identified with a system of ingenious excuses for combating either amelioration of working-class conditions, or drawing on a more ample reservoir of talent by expanding educational opportunities. I do not propose to justify this assertion in the present context, because it is copiously documented in what I have written on other occasions.

Another issue which helped to thrust the problem of nature and nurture into the foreground of social controversy was the emergence of new social machinery for dealing with a special class of human behaviour. In the eighteenth century the idiot and the lunatic were objects of derision and abhorrence, roaming at large or confined in conditions similar to the worst jails of the time. Eventually their condition was forced on the attention of the legislature by the growth of humanitarian sentiment and the exigencies of urban concentration. In Britain and in America those who took an active part in promoting new institutions for the care of the mentally defective or deranged were generally inspired by philanthropic zeal which drew little inspiration from scientific knowledge. A citation from Penrose's book on *The Mental Defective* conveys an attitude which was commonly accepted by them. It is taken out of one of the earliest reports of Park House, Highgate, the first asylum for "idiots" in Great Britain:

> We ask that he may be elevated from existence to life—from animal being to manhood—from vacancy and unconsciousness to reason and reflection. We ask that his soul may be disimprisoned; that he may look forth from the body with meaning and intelligence on a world full of expression; that he may, as a fellow, discourse with his fellows; that he may cease to be a burden on society, and become a blessing; that he may be qualified to know his Maker, and look beyond our present imperfect modes of being to perfected life in a glorious and everlasting future!

When the course prescribed by the pious founders of the new institutions failed to reinstate the victims of their benevolence as acceptable members of society, opinion swung to the opposite extreme, and the naively optimistic view that defective neuromuscular development can be cured by reading the Bible prepared the way for a fatalistic insistence on sterilization as a panacea for social betterment. The voluptuous enthusiam with which the Eugenic movement espoused the cause of mutilation is attested by a flood of literature too copious to merit further comment. The truth is that the new fashion had as little foundation as its predecessor in firmly established scientific knowledge. In different fields of social discussion both views continue to flourish. Educational reformers with radical views often justify them by arguments which suggest that caterpillars of the cabbage butterfly will thrive on a mixture of pollen and honey. Their opponents appear to hold that Newton would have written his *Principia* if he had been born in Tasmania. While other branches of natural knowledge have been nursed by social demands for the satisfaction of common needs which are endorsed by general consent, the study of human genetics, more especially in relation to social behaviour, has been the focus of partisan controversies in which common sense and curiosity have been continually stifled by political passions.

The genetic analysis of social behaviour

The study of intelligent behaviour among human beings from the genetic standpoint has been retarded by intrinsic difficulties apart from extrinsic obstacles to progress inherent in the social background of the subject. One arises from the fact that genetical research on human beings is beset by many difficulties which do not arise in the study of animals or plants

under standardized laboratory conditions. The other arises from the preliminary need for recognizing and classifying significant features of intelligent behaviour and for devising standardized tests to measure and record them. The primary difficulties which beset genetic analysis of variation within the human species are that human matings cannot be arranged by the investigator, and human offspring do not mature in circumstances which the investigator can control. Of its very nature social behaviour depends on an environment complex which cannot be standardized. Individual differences of social behaviour, as we observe them, are differences to which differences of environment and gene differences jointly contribute. For this reason the detection of differences due to the action of single genes or of relatively simple combinations of single genes is extremely difficult, and a more general issue claims prior attention.

When differences of environment and differences of gene equipment jointly contribute to observed differences between human beings it may be that genes responsible for a trait are rare (or are mainly confined to a small group of people), while the conditions of nurture on which their detection depends are relatively common. Heredity is then the more significant source of variation. Conversely, it may be that the responsible genes are widely distributed in the population, while the relevant conditions of nurture are rare or very unevenly distributed. The more important source of variation, then, resides in the environment. In this sense we are entitled to ask whether nature or nurture is the more *important* agency which determines individual differences. When it is not possible to find out which decides the fate of a particular individual the question can still be investigated on a statistical scale. Of several methods which can be used the three most general ones are (*a*) the method of twin resemblance, (*b*) the method of adoption, (*c*) the method of consanguinity.

The method of twin resemblance was first suggested by Galton. Partly because the pertinent facts were not fully established and partly because there were insufficient endowments to support large-scale research, it has not been applied extensively till recent years. The fact that twins may be of two kinds, *monozygotic* twins which have the same genetic constitution and *dizygotic* twins which are not more similar than ordinary sibs from the genetic standpoint may be used in two ways. We may compare the degrees of similarity shown by identical twins, fraternal twins, and ordinary "sibs" (brothers or sisters) brought up together in the same family, and we may compare the resemblance of identical twins reared apart with that of identical twins brought up together. If identical twins are decidedly more alike than fraternal twins brought up in the same family, we may conclude that heredity plays a large part in deciding the difference between individual members of *a single family*. If fraternal twins are decidedly more alike than ordinary sibs, we may conclude that the differences of environment to which children of different ages, brought up in the same family, are exposed, play a large part in deciding the characteristics of individual members.

Too little attention has been paid to this limitation of the twin method. Since the environment of a family at one social level may be very different from that of a family at another, the discovery that heredity is the chief agency which decides what the characteristics of different members of the same fraternity will be, does not necessarily imply that it is the chief agency which decides differences between individuals belonging to different social classes, races, or religions. This can be settled by comparing the degrees of similarity shown by identical twins reared together and identical twins reared apart in totally different social circumstances, as happens when they are adopted at birth, because their parents die or desert them. The interpretation of twin differences is also subject to limitation due to the fact that the genetical constitution of a human being plays a part in deciding the sort of environment in which social behaviour is conditioned. Thus the very fact that identical twins are inherently more alike than fraternal twins signifies that they are more likely to choose the same or similar associates. Although it is true to say that the genetic constitution of fraternal twins is less alike than that of identical twins, it is not equally true to say that the environment of fraternal twins is as uniform as the environment of identical twins. Hence it is not legitimate to argue that greater similarity of identical twins is wholly due to the *direct* relation of their genetic make-up to specific characteristics which they share.

The practice of adoption furnishes other opportunities for genetic inquiry. If true sibs reared together are decidedly more alike than true sibs reared apart, or if foster sibs are more alike than pairs of individuals taken at random from similar homes, differences of home environment may be inferred to play a decisive role. A third method of investigating the role of nature and nurture depends on the theory of inbreeding. Inbreeding results in separating *pure* stocks from a hybrid population. Hence it increases the variance, and a high measure of variability among children whose parents are consanguineous when compared with children whose parents are not related points to the influence of nature rather than of nurture. In contradistinction to comparison of the offspring of normal and consanguineous unions the study of resemblance between males or between females when they are (*a*) maternal cousins, (*b*) paternal cousins, and (*c*) mixed cousins, provides a means

of detecting the specific influence of sex-linked genes. This test depends on the fact that male paternal cousins share no *X*-borne genes. Hence from the standpoint of sex-linked inheritance male paternal cousins are less alike than male maternal cousins. When the manifestation of a trait can be shown to be related to order of birth or maternal age, we may infer the influence of uterine environment or changing conditions of family practice. The converse is not true. Failure to detect such a relation leaves us where we were before.

These methods of attack have been elaborated within the last twenty years. That they have been applied to the study of comparatively few aspects of man's social behaviour is chiefly due to two circumstances. The first is the persistence of the studbook mentality which is illustrated by the Lidbetter pedigrees and by Dr Hurst's memoirs on the inheritance of intellectual ability. The overwhelming majority of publications ostensibly dealing with human heredity are collections of pedigrees. The analysis of pedigrees can supply useful information when the data contained in them satisfy numerical tests suggested by the known behaviour of genes. The fact that they pass the tests justifies the suggestion that ordinary differences of environment do not interfere with the expression of the gene difference. So the conclusions drawn from them are irresistible. When the data supplied by pedigrees fails to do so we are in doubtful territory, and the more so when we are studying social characteristics such as temperamental traits and intellectual performance, which are known to demand certain limiting circumstances of upbringing. The studbook is a reliable guide to the inborn qualities of pedigree cattle, because the farmer aims at equalizing the environment of individuals selected for parenthood. For two reasons it is not a reliable guide to the contribution which heredity makes to differences of behaviour. One is that the human family transmits a certain social tradition, i.e. a particular sort of environment as well as a certain equipment of genes. The other is that equality of environment is not recognized as a goal of social organization by most eugenists.

The measurement of intelligent behaviour

While it would be difficult to discover any single criterion which is generally recognized when the adjective *intelligent* is applied to the social behaviour of adult human beings, there is a sense in which most people use it when they speak of the behaviour of children. Performance of scholastic tasks is generally accepted as a standard for classifying children as more or less intelligent, and the standardization of tests which eliminate handicaps or advantages due to formal instruction when different groups of children are tested by ordinary scholastic examinations makes it possible to make comparisons from a large reservoir of relevant material. Different observers can then arrange a group of individuals on a scale of what they call greater or less intelligence. Extensive and careful statistical researches have now been undertaken to devise a scale which will record what is *common* to the various ways in which people use the word *intelligent*, when we apply it to the social behaviour of children and adolescents. It does not necessarily follow that intelligence tests on which this scale is based give a just measure of all that we commonly mean by the adjective *intelligent* when we apply it to adults. Probably the intellectual performance of adults depends quite as much on temperamental characteristics ordinarily described by alertness, persistence, curiosity or a sense of humour as on the type of facility which intelligence tests assess. Hence proposals to limit educational facilities to children who get high scores in such tests are exceedingly dangerous, and since it is never suggested that the education of the prosperous classes should be limited in the same way, the political motive for the demand is not far to seek.

The great advantage of the tests on which the I.Q. is based is that they yield very constant results for the same individual examined on successive occasions if the intervening period is short. They also give fairly constant results for the order of individuals within a group when it is tested successively over a period of several years. This relative constancy of the I.Q. has given rise to exaggerated claims for the genetic status of tests for assessing it. It is still commonly asserted that the ordinal position of an individual's test score in a given group is a fixed characteristic, and that it must therefore be predetermined by genetic constitution. The first statement is untrue and the second is inconsequent. The fact is that the I.Q. is not constant throughout life. By their very nature the tests used to assess it cannot be applied to individuals until several years after birth. It cannot therefore take account of the formative influence of the uterine environment or of the conditions of life during the first three or four years of existence. Thereafter the results of repeated observation tests upon the same group when carried out over a period of several years have shown that the correlation of successive test scores is significantly lower than it is when the interval does not exceed more than about eighteen months. Before the age of four the neuromuscular organization of a child may be impaired in various ways by the accident of epidemic diseases such as mumps or scarlet fever. It should therefore be unnecessary to insist that even if the observed constancy of the I.Q. were perfect, it would tell us nothing about the contribution of genes

to variations of the kind which are recorded by intelligence tests.

In the light of knowledge derived from experiment on animals it is now clear that this question can only be settled by using methods such as those which have been outlined. Efforts directed to this end are comparatively recent, and more work remains to be done before it is possible to justify confident conclusions about the contribution of genes to I.Q. ratings. The largest scale inquiries have been concerned with the resemblance of twins brought up together and the resemblance of foster sibs or of sibs adopted in different homes.

About one aspect of the resemblance of twins reared together all observers are unanimous. Identical twins are much more alike than fraternal twins. There is less unanimity about whether fraternal twins of like sex significantly resemble one another more closely than mixed twins; or whether fraternal twins of either type are more alike than sibs of different ages. When due allowance is made for the limitation inherent in the twin method the recorded facts point strongly to the conclusion that genetic variation makes a large contribution to I.Q. ratings of *offspring of the same parents when brought up in the same home environment*.

For reasons previously stated this does not mean that genetic constitution plays an important part in variation of I.Q. among individuals *from different homes at different social levels*. Up-to-date a comparatively small sample of identical twins reared apart is available to throw any light on this. So far as they go the available data indicate that the mean differences of identical twins apart are of about the same order as the mean differences of fraternal twins reared together. If this proves to be true it disposes of the claim that I.Q. differences in a mixed population are a satisfactory measure of inborn capability.

Extensive observations on foster sibs or on sibs of different ages adopted into different homes have yielded different results. This fact does not necessarily signify that the work of one investigator is more reliable than that of another. The social circumstances of adoption vary from place to place. Among other things this means that the chance that sibs will be transferred to homes which are more or less alike is an accident of locality. The maximum difference between sibs reared apart or the maximum resemblance of foster sibs reared together is more relevant to a correct judgement about the role of nurture and nature than the minima recorded by other observers who select their material from a different source.

So far there have been no comprehensive studies on the variance of children with parents who are themselves first cousins or are otherwise related. Comparisons of I.Q. correlations for male pairs or female pairs of maternal and paternal cousins reveal no differences which point to the influence of sex-linked genes. There does not seem to be any significant relation between I.Q. and maternal age or order of birth to suggest the influence of uterine environment or the changing fortunes of family life. The data at present available suggest that genetic constitution plays a large part in determining I.Q. differences between individuals brought up in the same family, and that environment plays no mean part in determining I.Q. differences between individuals brought up in different families at different social levels. We shall be able to state these conclusions with more confidence and precision when large-scale investigations on twins reared apart, more research upon the resemblance of foster sibs, and new inquiries on the offspring of consanguineous parents have been undertaken.

In the meantime the chief obstacles to progress in the study of social behaviour from the genetic standpoint arise from the limited number of reliable quantitative tests for recording the more complex aspect of intelligent behaviour as we observe it in *adult* life, and from a lop-sided view of the practical value of such investigations. No useful purpose is served by minimizing difficulties which can be overcome only if generous endowments are available for larger scale field work than has yet been undertaken, and a less doctrinaire temper prevails when the results of such inquiries are discussed.

When human genetics is subsidized to advance the fullest use of human talents without regard to race or social class, it may be possible to detect and to measure group differences of intelligence depending upon differences of genetic constitution. Since it is not consonant with the temper of genuine scientific inquiry to assume that a single race, class or nation has the monopoly of all the virtues, a truly scientific approach to the problem is only possible when the investigator is prepared to forgo the moral luxury of assuming that the characteristics of his own social group are necessarily superior. Fortunately the temptation to do this will be less when psychology can equip biological research with a sufficient variety of similar methods for the precise description of other aspects of social behaviour. One can assert that deaf-mutism is commoner among Jews than among Gentiles without incurring the charge of anti-Semitism. With so many diagnosable physical ailments to choose from, it is possible for normal people to discuss the occupational or racial distribution of any single disease of the body without assuming a tone of impudent superiority.

So far the only social impetus to the study of human genetics, especially in so far as it is concerned with the part played by heredity in social behaviour, has come from proposals for restricting educational

expenditure or public money spent on institutions for the care of its defective members, from policies concerned with commercial exploitation of backward peoples, and from the psychological frustration which has accompanied the acceptance of sterility as the cardinal virtue of the middle classes. In Britain and in America the eugenic movement has recruited its advocates from the childless rentier, twentieth-century Bourbons who have earned nothing and begotten nothing. Its voluptuous insistence on mutilation as the goal of applied genetics has borne fruit in no outstanding discoveries. Human genetics has not yet discovered an incentive sufficient to guarantee its further progress.

The study of human inheritance has everything to gain by outgrowing the castration complex. With the prospect of a spectacular decline of population in the near future constructive statesmanship will be more and more preoccupied with ways and means to encourage parenthood. Consequently it will be less and less favourable to drastic proposals for sterilizing the harmlessly unfit. For the same reasons it will be more and more committed to an active policy of preventive medicine. As part of an active policy of preventive medicine the future of human genetics is assured. No community is likely to sterilize people who suffer from frontal sinus infections, or to subsidize research which leads to the conclusion that people who suffer from sinus infections should necessarily be sterilized. What makes it important to know everything which can be found out about the contribution of heredity to such diseases is that if we have such knowledge we can forewarn people who are liable to contract them against exposing themselves to the dangers of infection. So long as sterilization is the practical goal of human genetics its scope must be limited to the study of comparatively serious disorders. As a department of preventive medicine it embraces the whole field of disease, and brings a new method of approach to the analysis of clinical entities which would otherwise be difficult to distinguish.

A recognition of the social value of human genetics also demands a new orientation to educational policy. The writings of eugenists abound with assertions about the "waste" of expenditure on those who are "by nature" unable to benefit from it. Naturally, this does not engage the sympathy of educationists who take their job seriously. Nor does it enlist the support of intelligent citizens who realize that no society is safe in the hands of a few clever people. If knowledge is the keystone of intelligent citizenship, the fact that many people do not benefit from existing provisions for instruction is less a criticism of themselves than a criticism of educational machinery. The possibility that heredity plays a large part in such differences is only relevant to public expenditure, when we have already decided whether we want more or less education. We do not need biologists to tell us that any subject can be made dull enough to defy the efforts of any but a few exceptionally bright or odd individuals. By exploring individual differences human genetics might help us to find out how to adapt our educational technique to individual needs. It will do so, and gain prestige in consequence, when it ceases to be an apology for snobbery, selfishness and national, racial or class arrogance.

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HOLLAENDER, A. ***Wave-length Dependence of the Production of Mutations in Fungous Spores by Monochromatic Ultra-violet Radiation*** **(2180–3650 *A*).**

Genetical changes in spores of typical dermatophytes were studied (in co-operation with Dr C. W. Emmons) after exposure to monochromatic radiation at twelve wave-lengths between 2180 and 3650 A. The technique used insured that on the average each spore received and absorbed definite quantities of energy. Survival ratios were determined from plate counts for the different wave-lengths tested.

Micro-organisms have certain advantages for the study of the genetical effects of ultra-violet radiation, since they do not offer any serious obstacles to the penetration of the ultra-violet to the chromatin; they can be handled in large numbers. However, our knowledge of their genetical make-up is meagre.

Spores surviving irradiation showed several definite modifications: (1) non-genetical, (*a*) morphological, (*b*) physiological; and (2) genetical. Morphological and physiological changes would disappear after a few transfers.

The spores investigated here are uninucleate as well as unicellular (no sexual stage known). Permanent variations or mutations may appear in old cultures, but the spores used in these tests came from young cultures, and in the more than 3000 controls used in this investigation not a single mutation appeared. Mutations induced by ultra-violet radiation in these spores differed from the normal in colony size, colour, appearance of mycelium, spore production and growth rate. These changes are permanent since no reversal was observed after twenty transfers.

The highest rate of mutations in surviving organisms was more than 20 %. 10 % mutation can be obtained with greatest regularity. If one plots the energy received per spore against the percentage of mutations in surviving spores, one observes with increased energy, first a straight line, then a levelling up of the

mutation rate, and finally a decreasing number of mutations produced. There seems to be a close relationship between the fungicidal action of the radiation and mutation production.

Plotting the efficiency of the different wave-lengths against the wave-length, we find that we have two maxima, one at 2650 A. and a lower one at 2380 A. No mutations were produced by radiations by wave-lengths longer than 3000 A. This wave-length dependence of efficiency of mutation will be discussed on the basis of absorption spectra of the possible chemical compounds in the cells, especially in the nucleus, the morphological structures and other physical factors modifying the action spectrum. These observations will be discussed in relation to ultra-violet photographs taken by Dr Peter A. Cole at the different wave-lengths with the ultra-violet microscope and monochromatic radiation.

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HOWARD, ALMA and HUSKINS, C.L. ***Chromosome Studies in Mice***

Studies of chiasma frequency in young males of twelve distinct inbred lines of mice have shown that strains with a high incidence of spontaneous mammary gland cancer have low chiasma frequencies, while strains with low cancer incidences have high chiasma frequencies. Of the fifteen lines and sub-lines investigated, only one subline of one strain (Carrel's subline of C 57 Black) has been exceptional to this rule, and this subline has a doubtful cancer record, and the strain as a whole shows inconsistencies within itself. It is therefore concluded that a correlation exists between cancer susceptibility and chiasma frequency in mice.

Sufficient data are not yet at hand to determine whether this relationship is concerned with susceptibility to mammary gland cancer specifically, or to cancer susceptibility in general. One strain (C 58), having a high incidence of spontaneous leukaemia, shows a low chiasma frequency.

Extensive examination of the spermatogonial divisions of strains *A* (susceptible to mammary gland cancer, with low chiasma frequency) and *I* (resistant to mammary gland cancer with high chiasma frequency) revealed no difference between the strains in the time of splitting of the chromosomes at metaphase such as might be expected if this were related to chiasma frequency (see the hypothesis of Huskins and Hearne (1936)). The variability within each strain was, however, so great that this negative finding does not invalidate the hypothesis. The number of split chromosomes to be found at metaphase, before the beginning of anaphase separation, ranged from one to twenty per cell, with an average of about eight out of the total of forty. In the dividing cells of the germinal areas of lymph nodes also very widely split chromosomes may be found at prophase and metaphase. One or more of such widely split chromosomes was found in every lymph node and spermatogonial cell examined. This phenomenon has not previously been described.

Little (1933) found that when mouse lines having different susceptibilities to mammary gland cancer are crossed, the cancer behaviour of the offspring follows that of the maternal parent. In 1936 Bittner showed that this maternal influence is transmitted largely, if not entirely, through the milk which the young mouse receives from its mother. In view of the correlation which has been found to exist between cancer susceptibility and chiasma frequency, the behaviour of the chiasma frequency character in reciprocal hybrids between strains, and under the influence of milk from other strains, became a matter of particular interest.

Investigations on this problem have been carried out chiefly on strains *A* and *dba* (susceptible, low chiasma frequencies) and *I* and *JK* (resistant, high chiasma frequencies). Counts have been made of chiasma frequency in first generation hybrids from reciprocal crosses between these strains, and on mice of one strain fostered from birth on females of another strain. The relation of chiasma frequency to growth rate is also being investigated.

The results obtained have significance for the analysis and understanding of phenomena associated with the meiotic process, apart from their apparent relationship to the cancer problem.

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HUSKINS, C.L. and WILSON, G.B. ***The Structure of Chromosomes during Meiosis in*** **Trillium erectum** ***L.***

The meiotic and first pollen-grain divisions of *Trillium erectum* have been studied in order to determine: (*a*) the general structure and behaviour of the chromosomes during these divisions; and (*b*) the properties of, and the phenomena associated with, the major coil of meiosis and the relational twisting at prophase and metaphase of first pollen-grain division.

The results of general studies are in agreement with those reported by Huskins and Smith (1935).

Studies on major coil gave the following results:

(*a*) The chromonemata about double their length during coiling while the chromosome contracts slightly.

(*b*) The direction of coiling can change at the attachment and within the arms.

Analysis of the frequency of these changes shows that they are due to the attachment, chiasmata, and some factor the effect of which is proportional to the number of gyres. The first two of these factors are points of interference on either side of which the direction of coiling is random. From these data it is suggested that coiling may be due to the elongation of the chromonemata within a limiting membrane or pellicle.

The following data have been obtained from studies on relational twisting:

(*a*) The direction of coiling is approximately random on either side of the attachment.

(*b*) The frequency of reversals within chromosome arms is about the same per twist as the frequency of changes in direction per gyre of the major coil.

(*c*) The number of twists per cell varies directly as the total length of the five chromosomes, and is decreasing during contraction.

From these results it is suggested that the major coil and the relational twisting are related in origin in that the latter is due to the tendency of the half-chromatids to twist about one another during coiling in such a way as to compensate for the spiral.

The following hypothesis of coiling is presented: a differential length change between the chromosome (pellicle) and a split chromonema may be expected to result in a spiral coil and a compensating twisting of the half-chromatids. On uncoiling of the spiral the latter would become a relational twist.

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HUSKINS, C.L. and NEWCOMBE, H.B. *Chromatid and Chiasma Interference in* Trillium erectum *L.*

Preparations of first meiotic metaphase of *Trillium* have been obtained in which chromatid structure is sufficiently clear to allow the space relationships of all four strands of a bivalent to be traced. The frequencies and average lengths of the eight cytologically distinguishable types of chiasma pairs have been determined for forty-eight complete cells.

The frequencies of these types are not those which would be expected on any of the current theories of crossing-over. The chiasma pairs involving the attachment showed an excess of the non-compensating type, but the number of such observations was too small to be certain that the proportion differed significantly from that found in the arms. The types occurring least frequently are those having the greatest number of chromatid twists between chiasmata. These also tend to have the greatest average lengths. This would indicate a certain amount of chromatid twisting in existence at the time of crossing-over.

Coincidence of chiasma formation is greater than unity across the attachment. Coincidence within the arms varies as the distance between chiasmata, reaching a value considerably exceeding unity. An increase in chiasma formation is accompanied by increased coincidence within the arms and decreased coincidence across the attachment.

Table 1. *Frequencies and lengths of the different types of chiasma pairs*

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	Totals
	Frequencies								
Melanoplus (Hearne and Huskins)	27	26	9	3	.	.	.	.	65
Trillium (preliminary data)	33	15	1	1	.	.	.	.	50
Trillium (main data)	190	144	34	16	3	2	1	1	391
Totals	250	185	44	20	3	2	1	1	506
	Average lengths in microns								
Melanoplus	3·5	4·8	5·1	3·9	.	.	.	.	
Trillium (preliminary data)	2·3	3·3	5·7	3·1	.	.	.	.	
Trillium (main data)	2·5	3·7	3·6	4·7	4·0	3·0	10·0	10·0	
							5·4		

Possible implications of these data are discussed, and a hypothesis of crossing-over is presented.

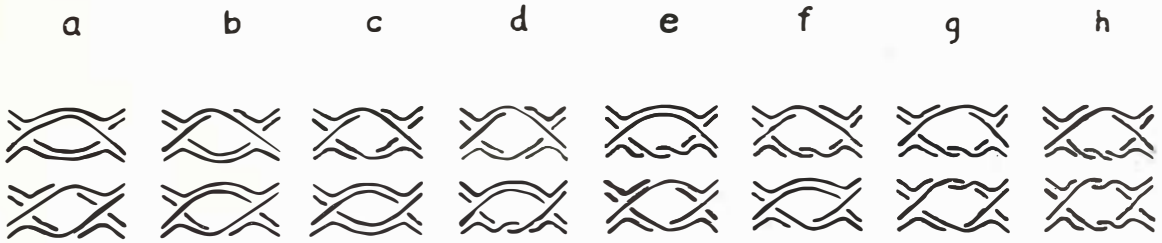

Fig. 1. Diagrammatic representation of the eight cytologically distinguishable types of chiasma pairs observed in *T. erectum*. Each type is represented in two ways, with the two chiasmata in opposite directions (top row), and with the two chiasmata in the same direction (lower row). The two representations of each type cannot, of course, be distinguished cytologically.

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HUTCHINSON, J.B. ***The Genetic Interpretation of Plant-breeding Problems***

The influence of genetics on plant breeding has been much less profound than expected by the early geneticists, because the study of the inheritance of quantitative characters with which plant breeding is primarily concerned has so far remained undeveloped. The object of the present paper is to survey the application of genetic theory to cotton breeding in particular, and to outline the outstanding genetic problems underlying breeding practice.

It is clear from data available that in cultivated crops natural and human selective forces tend to establish a balanced mixture rather than a single type to the exclusion of others. This emphasizes the importance of studying the genetics of heterogeneous populations. While uniformity in a crop has agricultural advantages, genetic variability is necessary to ensure a flexible response to environment, and the breeder must set an upper limit to the standard of uniformity desirable in his strains. It must also be realized that breeding has to be a continuous process to maintain this uniformity against the tendencies in the opposite direction.

Another problem is a detailed physiological-genetic analysis of the interrelations of the component characters of a plant. A character under selection is frequently made up of several components, a proper balance amongst which must be maintained during the breeding process.

Following Vavilov's discovery that variability in cultivated crops is maximum at the centres of origin of the several species, these small areas are properly the sources for collecting material in which to select. It should be noted, however, that in regions situated in the neighbourhood of such areas, no collection of types brought from outside can compete with the native variability of the local unselected crops. Cotton in India, with three centres of origin of two species in the country, is an example. Guidance in the use of hybridization as an alternative source of variable material has become available to cotton breeders in the light of Harland's theory of genetic balance and Hutchinson and Ghose's reclassification of the genus.

In the technique of selection, progeny row breeding in the place of mass selection was the first important improvement. Experimental designs based on modern statistical methods have recently been applied to progeny row breeding by Hutchinson and Panse. These have proved very successful in reducing the environmental contribution of variance and have made the detection of very small differences in the earliest stages of breeding possible.

Studies on the rate and magnitude of change that can be induced by selection have an obvious bearing on breeding policy, but only a few recent papers have been devoted to the subject.

Some of the problems outlined here fall outside the scope of genetics as it is now studied, and the development of a branch of applied genetics to cover the theoretical ground of breeding problems is important.

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HUTT, F.B. ***The Association of Physiological Traits with Breed Characteristics in the Fowl***

Breeds of domestic birds are differentiated during their formation by size, conformation, structural variations, colours and feather patterns. To effect this differentiation, a great assortment of mutations have been adopted as breed characteristics. These even include lethal genes, e.g. in the Creeper and Cornish Indian Game fowls, the Crested ducks and the Rosy Gier pigeons. Since the days of Columella it has been customary for poultrymen to ascribe all manner of economic virtues to their favourite breeds, but breeds in which a valuable physiological trait was deliberately incorporated as a breed characteristic are (with one possible exception) unknown. A number of such characteristics have recently been discovered many years after the establishment of the breeds with which they are associated.

In comparison with such heavier breeds as Rhode Island Reds and Plymouth Rocks, the White Leghorns need less vitamin B_1 and are less subject to slipped tendon, or perosis, a condition with a genetic basis which indicates an abnormally high requirement of manganese. Leghorns are more resistant to *Salmonella pullorum* but more susceptible to *Ascaridia lineata*. That the Leghorns can better regulate body temperature is shown by their greater resistance to extreme heat, and the fact that after hatching the body temperature rises to the normal range for adults more quickly in Leghorn chicks than in Rhode Island Reds. White Leghorns lay eggs with somewhat denser shells than those of heavy breeds. Female Leghorn embryos are converted to intersexes by less androsterone than are embryos of heavy breeds. Single combs in Mediterranean breeds respond more readily to male hormones than single combs in heavier breeds.

These physiological traits, many of them economically valuable, are inherited characteristics as much as any structural modification or colour. They are not directly related to differences in body size of the breeds compared. They might result from linkage of a gene for a physiological character with one for some morphological variation adopted as a breed charac-

teristic, or from pleiotropic action of a gene of the latter type. However, it seems more probable that these differences are not merely between Leghorns on the one hand and Rhode Island Reds or Plymouth Rocks on the other, but rather between Mediterranean breeds and descendants of Asiatic breeds. They may have resulted from exposure of these races to different environments after domestication. Apart from that possibility, these physiological differences suggest that the Asiatic and Mediterranean races are descended from different ancestral species and thus greatly extend the previously recognized evidence for a polyphyletic origin of domestic fowls.

In a different class is the lowered capacity for reproduction associated with breed characteristics of the White Wyandotte. This has long been suspected but only recently proven. It is still not clear whether the proportion of eggs fertilized is subnormal or whether embryonic mortality at a very early stage is unusually high. There may be linkage of a lethal gene with one of those determining breed characteristics, or pleiotropic action of some of the latter may be responsible.

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HUXLEY, J.S. *Evolutionary Genetics*

Classical genetics has demonstrated the complex particulate nature of the hereditary outfit and its quantized method of change by mutation. Cytogenetics has unbared the chromosomal machinery involved in hereditary transmission, its basic similarity throughout all multicellular organisms, and its important variations in detailed construction. Physiological genetics, though still in its infancy, is busy with an analysis of the dynamic relation between gene and character in individual development. And now geneticists are attacking the other great dynamic problem—the relation between genetic machinery and the processes of evolutionary change and taxonomic diversification.

This latest branch of our subject we may perhaps style evolutionary genetics. Much has already been accomplished in this field by way of analysis and induction. It seems to me that the time is ripe for far-reaching synthesis and deduction as well. Such an approach is bound to clarify principles underlying taxonomy, which, after all, is a description of the results of evolution; and this in its turn will assuredly lead to the discovery of many new facts which will not merely illustrate but enrich genetic principles. Much pioneer work has already been done in this field. I need only mention such names as Vavilov, Fisher, Dubinin, Wright, Timoféeff-Ressovsky, Haldane and Dobzhansky; while Darlington's recent book on the *Evolution of Genetic Systems* is a bold essay in deduction in this subject.

Darwin's work was perhaps the most notable example of the use of the combined inductive-deductive method in biology (see discussion in Huxley, 1938*a*). I believe that we may now look forward to a renewed employment of similar methods in the same field. In the brief space at my disposal it would be foolish to attempt a survey: I can merely point out a few of the lines along which knowledge has progressed, and some of the ways in which the two branches of biology, taxonomy and genetics, each with its own vast body of data and its own principles, can mutually fertilize each other and merge into a unified science of evolutionary genetics.

All life is, owing to the nature of reproduction, in a certain real sense a continuum. Yet its most obvious feature is discontinuity: it is cut up into discontinuous individuals and discontinuous groups. The central problem of taxonomy is that of the discontinuous groups we call species. How does this discontinuity originate and how is it maintained? The answer is isolation. Granted mutation and selection, isolation will automatically produce some degree of divergence of the isolated groups. When conditions are markedly different, selection will see to it that the groups diverge adaptively. But even when the environment does not provide this necessary basis for divergence, divergence will none the less automatically occur, though it will naturally proceed at a slower rate. In such cases, divergence will occur owing to the accumulation of mutations, which on the theory of probability are bound not to be identical (Muller, 1939). Even when an adaptive trend is similar in two groups, the mutational building blocks employed to give it effect will differ, so that in process of time the gene complexes of the two isolated groups will become stabilized in different ways. This will lead to an increase of isolation between the groups, which will become less compatible on crossing. The incompatibility may reveal itself in lowered viability of offspring, owing to the disharmonic nature of the gene combinations formed by crossing, or in lowered fertility, or actual sexual incompatibility of the parents. Once this stage is reached, then, provided the two groups overlap so that crossing may occur naturally, selection will step in to make crossing more difficult, since it will result in reproductive waste.

Isolation is thus itself a cause of divergence, and may become a self-reinforcing process.

This automatic or intrinsic divergence is only non-adaptive in the sense that it is at the outset not associated with divergent adaptation (though later sometimes reinforced by reproductive adaptation). The evolutionary processes of the diverging stocks

may and in general will be themselves adaptive, both as regards the characters of the individual organisms and the harmonious stabilization of their gene complexes.

When the size of an isolated population is small, however, then, as Sewall Wright (1939) has shown, truly non-adaptive differentiation will occur, in the sense that neutral or even deleterious mutation and combinations will become fixed in its constitution. We must thus distinguish between non-adaptive divergence between two or more groups, which is universal but non-adaptive only *qua* divergence, and non-adaptive differentiation of single groups, which is non-adaptive in itself, though it will also lead to non-adaptive divergence from other groups, but only operates in populations below a certain effective breeding size.

This non-adaptive differentiation leads to much diversification of life which is irrelevant to the major or long-range trends of evolution, and accounts for the fact that subspeciation and speciation is much more intense on islands than on continents, in lakes than in oceans. A detailed empirical confirmation of the principles has recently been given by Kramer and Mertens (1938) for insular lizard populations in the Adriatic.

Another mode of accidental diversification is by non-representative sampling. When a relatively isolated area is colonized by a few individuals only, it is improbable that these will be average representatives of the population from which they spring. When this population is itself very variable, the divergence may be striking. This process seems to have played a considerable part in generating the diversity shown, e.g. by the local groups of land snails in Tahiti and other Pacific Islands (Crampton, 1916, 1932); here, for instance, local groups may be either all sinistral, all dextral, or of mixed type.

The importance of isolation in generating accidental (non-adaptive) divergence is shown by the frequency of differences in sectional arrangements of chromosomes between different species. These are all biologically improbable, in the sense that there cannot in the great majority of cases be any selective advantage inherent in any new rearrangement, and that they can only be expected to become fixed as frequent or typical components of a group by some accident associated with isolation. Yet, though this must be rare by ordinary standards, it becomes frequent in the perspective of geological time, even in the relatively short periods needed for speciation within a gene.

Returning to adaptive divergence, we find that both the degree and type of divergence will differ according to circumstances. Among the relevant circumstances may be mentioned the type of isolation; the degree of overlap of groups, the mode of life of the evolving organisms, and the intensity of the selection pressure to which they are subjected.

Let me take a few examples to illustrate these points. When genetic isolation has introduced incompatibility between two groups, as between *Drosophila melanogaster* and *D. simulans*, for instance, and the two groups continue to inhabit the same general region and to lead the same type of life, there will be little selection pressure tending to cause divergence of the two, and their differentiation is likely to be slow and accidental. We shall therefore expect to find what has been called cryptic speciation, in which species that are perfectly "good" from the biological standpoint are by ordinary standards almost indistinguishable, and would, in fact, not be distinguished even as subspecies were it not for the experimental evidence. It is likely that the number of such cryptic species will be considerably enlarged as experimental analysis is extended.

The same sort of thing is likely to occur with so-called physiological races—i.e. groups adapted to different hosts or different food plants. Here, however, the isolation appears at first to be maintained, as Thorpe has shown, largely by modificational means, the host preference of the adult being influenced by its earlier experience as larva and on emergence. Selection will later be expected to accentuate divergence, partly in the form of what Baldwin (1902) and Lloyd Morgan (1900) called organic selection, the lability of preference based on experience being replaced by the more rigid basis of innate preference, and the groups becoming also more highly adapted physiologically to their hosts, and partly in the form of reproductive selection, barriers being erected to intercrossing so as to obviate waste. Though adaptively different in behaviour and physiology, however, the types will remain very similar in appearance, and will tend to be taxonomically neglected until experiment forces them upon the systematist's attention.

Another interesting contrast will evolve between geographically isolated and non-overlapping groups on the one hand, and on the other those that have diverged ecologically and have geographically overlapping ranges. In the former there is no opportunity for intercrossing, since space is sufficient barrier; but in the latter intercrossing may occur and is a biological danger to be guarded against, since its products will *ex hypothesi* be less well-adapted than either parental type. Accordingly we may expect to find that in the cases of geographical divergence reproductive isolation will arise slowly, as an accidental consequence of the isolation, while in the overlapping but ecologically divergent group special barriers to intercrossing will be evolved. These themselves will add

to the difference between the groups, so that in general the degree of divergence achieved in a given time will be greater.

The taxonomic bearings of this fact will differ according to the type of organism and its mode of life. Thus in plants, reproductive isolation may be achieved either by a difference in time of flowering, or by adaptation to different insect pollinators: the latter is likely to involve obvious taxonomic differences, while the former is not. Similarly in birds, in which group-reproductive barriers are usually concerned with sex recognition, related overlapping species which live in open habitats tend to develop visual differences (distinctive male plumage: cf. ducks, stonechat and whinchat, etc.), while in those frequenting dense cover the reproductive barriers tend to be auditory (distinctive song: cf. willow warbler and chiffchaff): the former is for purely practical reasons generally regarded as of more taxonomic value than the latter.

This last example leads on to another evolutionary effect of mode of life. Where the construction of the organism and its way of life is such as to encourage intermale competition, as in various types of birds, with their high level of nervous organization, their physical difficulty in coition and therefore need for synchronization of sexual rhythms, their territorial systems, etc., we shall expect to find the evolution of male characters of song, pattern, or both, which are at the same time conspicuous and distinctive (Huxley, 1938*b*).

Furthermore, these characters will often become partially transferred to the females. Thus, notably by the biological need for distinctiveness, the diversification of related species in birds will tend to be much larger than in groups without similar intermale competition; this diversification, while primarily affecting one sex only, will often affect both to some extent.

The effect of selection pressure is probably of greater importance than is usually realized. In some cases a natural experiment has been in operation, by which a group has been able to colonize certain areas in the absence of its chief predators. This has happened at least twice in the history of the Cichlids in the African Great Lakes, once in the early Cenozoic and again in connexion with the Pluvial Period (Worthington, 1937, 1939). In both cases the same result is to be observed. The degree of diversification of the Cichlids in the lakes where the chief predators (*Lates* and *Hydrocyon*) are absent is far greater than in those where they are present. Although such differentiation is chiefly a qualitative matter, it has its quantitative affect. This is brought out in Table 1, compiled from Worthington (1937, and additional data *in litteris*).

Although the very much greater length of time available for Cichlid evolution in Tanganyika has permitted a much more abundant radiation here than in Victoria-Kioga, and although almost all of the species are endemic, their number is little more than half that present in Nyasa, where the large predators are absent. In the other lakes, which must have lost all their fish fauna when they dried up in the interpluvial, those without predators show an overwhelming superiority in the number of their endemic Cichlids. Even the extreme alkalinity of Rudolf has failed to elicit a large Cichlid radiation in the presence of efficient predators. The difference between Victoria-Kioga and Edward-George appears to be due to the much greater environmental diversification of the former, and the partial isolation of the component lakes. The greater environmental diversity of Tanganyika as compared with Nigeria may have contributed to the relatively high number of its endemics.

It thus appears that tendencies which take the organism too far from the norm of the group, though they may be admirable for exploiting the environment, can be kept from realization by heavy predator pressure.

This phenomenon is familiar, in various modifications, throughout organic life. We have the evolution of flightless birds and giant tortoises in the absence of normal predators; or the great diversification often found in the rare groups which have managed to colonize oceanic islands, such as the ground finches (Geospizidae) on the Galapagos, here apparently owing to the absence of competition rather than to low predator pressure. On the largest scale, we have

Table 1. *Effect of predator pressure and environmental diversity on speciation of Cichlids in African lakes*

Lake	Date of isolation	Large predators	Environmental diversity	No. of endemic Cichlid species
Victoria-Kioga	2nd pluvial	−	++	58
Edward-George	2nd pluvial	−	+	18
Albert	2nd pluvial	+	±	4
Rudolf	Post-pluvial (*ca.* 10,000 B.C.)	+	−	3
Nyasa	Early (enozoic)	−	+	171
Tanganyika	Early (enozoic)	+	+	*ca.* 90

the formation, in the sheltered conditions of Australasia, of whole new families and order of marsupials, which were incapable of realization in the more competitive atmosphere of the rest of the world.

The nature of the organism, both as regards the structure of its genetic and reproductive system, its mode of growth and development and its general way of life, have equally profound effects upon evolution. The simplest and most clear-cut example is the difference between higher animals such as insects, birds and mammals, and higher plants such as the angiosperms. Higher animals have growth which is determinate in quality and often in quantity, without permanent growing points; no vegetative and (except in a few cases) no parthenogenetic reproduction; they possess a chromosomal sex-determining mechanism; the sexes must come together for reproduction; and there is usually provision by the parents at least for ensuring that the young shall find themselves in a suitable environment. Higher plants have indeterminate growth, with permanent growing points; are frequently capable of vegetative and/or apomictic reproduction in addition to sexual; with few exceptions, they possess no chromosomal sex-determining mechanism; sexual union is affected through pollination by wind or insects; and the securing of a suitable environment for the young plant is usually accomplished merely by the broadcast dispersal of seeds, many of which are bound to find themselves in unsuitable environments.

These differences between the two types have had extensive effects on their evolution (see Darlington, 1939). In the higher plants, the mode of growth, and especially the prevalence of vegetative and apomictic types of reproduction, permits the multiplication of rare mutations, including those like inversions, which are deleterious unless homozygous; they also permit the survival of conditions incompatible with sexual reproduction (such as triploidy and many forms of species hybridity), and of those associated with reduced sexual fertility (such as autopolyploidy), either permanently in an asexual phase, or until such time as chromosome doubling (in hybrids) or selection (in autopolyploids) restores sexual fertility. Meanwhile, the absence of delicately adjusted chromosomal mechanisms for sex determination makes it much easier for polyploids, both auto- and allopolyploids, to become established. The sudden formation of new species (by allopolyploidy), which is not infrequent in higher plants, appears never to occur in higher animals. The combination of apomixis and polyploidy, often with wide crossing also, which cannot be realized in higher animals, leads to the absence in animals of the taxonomically puzzling assemblages such as are found in certain groups of plants, like *Crepis*, *Rubus*, *Salix*, etc., where the ordinary concepts of taxonomy, such as species, wholly break down, and a reticulate may be substituted for a divergent process of descent (Turrill, 1936).

In regard to polyploidy, it is estimated that nearly half the species of flowering plants are polyploid (White, 1937), while in animals the proportion must be well under 1 %.

Finally, we have the curious contrast between higher animals and higher plants in regard to infraspecific categories. In animals, the tendency is to evolve well-defined subspecies, self-reproducing groups each occupying its own geographical area, or in some cases its own ecological niche, and showing at least partial biological isolation from their neighbours. In plants, on the other hand, though geographical subspecies undoubtedly do occur, the commonest kind of infraspecific differentiation seems to be into ecotypes. In any one region the population produces a large number of ecotypes, and in each habitat within the environment a small range of these is then selected (cf. Gregor, 1938). This mechanism differs radically from that of animals. The population of any habitat is not a self-producing group, but presents a restricted selection of a much larger array; conversely, the self-producing population of a large region is not similar throughout the region, adapted to the general regional environment, but is broken up by selection in each generation into a number of often very distinct groups, each adapted to detailed local environments. Such plants thus exhibit polymorphism, the different genetic types balanced by selective advantage; while higher animals are typically monomorphic, with restricted variance round a single adaptive mean.

A great deal of work remains to be done upon plant ecotypes, and undoubtedly different plant species will be found to differ enormously in the degree of this ecotypic polymorphism which they exhibit. But the difference from animals does seem to be a basic one.

In higher animals especially, the problems of subspeciation are themselves of extreme interest. Geographical subspeciation is the best-investigated and probably the commonest type, and I shall here confine myself to its results. It is just becoming clear that there exist two essentially distinct types of geographical subspecies according to their degree of biological discontinuity. In one type the discontinuity is complete, in the other it is partial. The former may be called independent subspecies, the latter dependent (Huxley, 1939*a*). There will of course be many cases where the assignment to one or other group is difficult to make; but in principle the two types appear to be distinct, since, as I shall attempt to show, they seem to represent different types of stable equilibrium.

Subspecies have often been styled "species in the making"; but this is true only of independent subspecies, such as are constituted by populations of land types inhabiting islands or of aquatic types inhabiting unconnected lakes. Doubtless some small degree of migration to and from islands may occasionally occur, notably with birds; but in general, if the barrier of sea is wide enough this is so slight as not to impair the biological independence of the group. It is an interesting fact that in general island populations of birds seem either to show no perceptible difference from the mainland forms (e.g. Orkney wren) or a quite distinct difference (e.g. Shetland wren) (see Witherby, 1938). It would appear that once the isolation reaches a certain critical degree, the isolated group is stabilized in a condition of full biological separateness or independence, which in the long run will result in divergence, largely accidental and non-adaptive, first of subspecific and eventually of specific magnitude. It is of course clear that factors such as degree of mobility will affect this result. Thus the degree of taxonomic differentiation of the mammals (mice and voles) of the Scottish islands from their mainland relatives is consistently higher than that of the birds. Again Rensch (1933) has shown that in birds the proportion of polytypic species (i.e. with geographical subspecies), and the number of subspecies per polytypic species increases rapidly with decreasing mobility (Table 2).

Table 2. *Degree of subspeciation in birds in relation to mobility* (*modified from Rensch* (1933)*; based on all species in Hastert's* Die Vögel der paläarktischen Fauna)

Type of bird	Monotypic species (without geographical subspecies) %	No. of subspecies (in the palearctic) per polytypic species
Large	54·5	1·6
Small, migratory	39·9	3·2
Small, non-migratory	20·6	7·2

With groups inhabiting large continuous areas, however, such as continental land forms (the conditions in corresponding aquatic groups are still obscure), matters are quite different. There will, of course, be cases where complete isolation and independence is achieved, through the operation of barriers such as large rivers, mountain ranges, etc.; but frequently, in spite of the absence of any such complete geographical barriers, the specific area will be divided into a number of definite subspecific areas, along the margins of which the subspecies will interbreed and intergrade. The discontinuity between such subspecies is thus only partial, and they are dependent on each other and on the whole species complex, in that a certain exchange of genes is constantly taking place between them. On the other hand, it is always characteristic of such systems that the intergrading zones are extremely narrow (often only a few miles) in comparison with the dimensions of the subspecific ranges (see e.g. Sumner, 1932; Miller, 1931).

The first thing to note about this type of subspeciation is that dependent subspecies need not be species in the making, and so far as we can tell will never (unless the physical barriers between them change) achieve specific rank. Actually, as Sewall Wright has shown, such a system, consisting of a number of locally adapted subspecies with a certain degree of gene exchange between them, provides the most favourable genetic structure for further evolution, with the greatest amount of potential plasticity. We can therefore assume that the subspecies within such a species will continue to evolve, but always as dependent subspecies within the system (Huxley, 1939*a*).

What we would also like to know, however, is how this peculiar condition originates, and is maintained in being. The principle of the stabilized gene complex appears to provide the answer. The discovery of modifiers capable of altering the expression of other genes led on to the realization that new mutations usually need adjustment by means of other genes before they could be profitably employed, and this again to the generalized concept of the gene complex, which must be regarded as an interacting whole, whose parts are stabilized in harmonious mutual adjustment.

Whenever a continuous interbreeding population is exposed to more than a certain degree of environmental difference, selection will promote external adaptation to the two or more extremes. But selection will further promote internal adaptation of the gene complex to the genes responsible for the external adaptation. The extra viability conferred by such a harmoniously stabilized constitution will cause the type possessing it to spread over a larger range than that to which it was originally adapted. Conversely, where it is in contrast with another similar type, the recombinations produced by crossing will in general be less viable and successful than either pure stabilized type, and accordingly the zone of intergradation will be kept narrow by selection (Huxley, 1939*a*).

There remains the question of how the separate differentiation of the two types with their two stabilized but distinct gene complexes comes into being in the first instance. It appears that it may do so in three rather distinct ways. First, by an incipient discontinuity due to a slight degree of isolation—the reduction of population density in an unfavourable area between the two main areas, or the interposition

of a barrier, such as a river, which slightly impedes while it does not prevent migration and intercrossing. Secondly, by a sudden alteration in environmental conditions, even without any barrier to free intercrossing, as occurs when mountains give place abruptly to plain, or woodland to open prairie. And thirdly, when what may be called the "biological tension", caused by the difference in environmental conditions, is large enough, it can be prophesied that this alone, even in the absence of zones of incipient isolation or of rapid environmental change, will bring about the differentiation into distinct stabilized types, and so of itself be sufficient to cause partial biological discontinuity. In any event, it is certain that the various zones of intergradation do not always correspond with zones of restricted interbreeding or of environmental change, as has been shown by Sumner (1932) in *Peromyscus*. Their present distribution may be entirely the result of biological tension, or they may have been shifted by migration.

In passing, the narrowness of the zones of interbreeding that exist between certain contrasted types which have met after differentiating in isolation, as for instance with the carrion and hooded crows (*Corvus cornix* and *C. corone*), depend on the same principle, of the greater viability (or fertility) of stabilized types than that of crosses between them (Meise, 1928). Here, however, the problem is not so difficult, since we have not to account for the differentiation of distinct stabilized types within an interbreeding continuum, but only in isolation.

The consideration of dependent subspecies thus forces us to recognize a subspecific stage of equilibrium within the differentiation process, in addition to the specific; a condition of *partial biological discontinuity* favoured in certain conditions, besides the other well-known favoured condition of complete biological discontinuity realized in full species.

It should be added that another interpretation of the facts is theoretically possible. It may be that the condition just described is not one of biological equilibrium, but is unstable, and that selection is destined to operate in such a way as to introduce reproductive barriers (in breeding habits or in sterility) between the subspecies that now interbreed freely, thus eventually abolishing the intergrading zones. On this view, what I have called dependent subspecies would not be permanent phases in the structure of the species complex, and would be "species in the making" as much as those which are geographically isolated.

On this view, which insists on sterility or mating barriers always being the product of selection, and never the result of chance accumulation of genes during isolation, the failure to interbreed in groups which have met after divergence in isolation, such as *Parus major* in the Far East, the two species of tree creeper, *Certhia familiaris* and *C. brachyrhyncha*, in Central Europe, or the nightingale and Sprosser, *Luscinia megarhyncha* and *L. luscinia*, in north Germany, must also always be due to the evolution by selection of special barriers to interbreeding in the region of overlap.

This latter conclusion seems to me unlikely. Further, the frequency of the existence of interbreeding subspecies with narrow zones of intergradation appears to indicate that this is not a temporary condition but a stable one. The general principle that *ad hoc* selection is needed for the evolution of mating or sterility barriers could be experimentally tested by crossing such extreme representatives of a chain of interbreeding subspecies as did not overlap geographically. If any of these exhibited mating or sterility barriers, the objection would fall to the ground. Meanwhile, the observational data of taxonomy appear to indicate the reality of dependent subspeciation as a condition of stable equilibrium.

To revert to the distinctions between higher animals and higher plants, we see that infraspecific differentiation is attained in the former by conferring internal adaptation upon a few gene complexes, enabling each of them to occupy more than the range to which it is in the first instance externally adapted, in the latter by providing numerous externally adapted types to compete for habitats within a region.

If this principle of partial discontinuity based on differently stabilized gene complexes proves to be as general in its occurrence as it seems to be on the basis of current taxonomic practice in describing subspecies in higher animals, it will explain yet another rather surprising fact, namely, the apparent absence or rarity of continuous change of character, at approximately the same rate, in conformity with continuous environmental change over large areas.

Such continuous character gradients, or clines as for brevity's sake I have suggested calling them, do occur. An excellent example is that of the common Nuthatch (*Sitta caesia*) in Central Europe (Løppenthin, 1932). An apparently undue number of the examples, however, are special cases—changes in the ratio of the two phases of a dimorphic species (e.g. the ringed variety of *Vira aalge*: Southern (1939)).

One would have expected at first blush that selection would cause character change to follow environmental change quantitatively, but apparently it does not do so; an organic discontinuity appears to be superposed upon the inorganic continuity in taxonomy, just as it is in ecology, where plant communities end with a surprising sharpness, as at timberline in the mountains (Elton, 1927, Ch. 1).

If this be really established, it will, as I have said, be due to the principle of stabilized gene complexes. The extension of these over areas greater than that to which the complexes developed their primary external adaptation will obviously flatten out any cline in the large (subspecific) areas, and steepen it in the small areas or of the intergrading zones, converting the continuous slope into a staircase.

As a matter of fact, such a staircase is frequently found—for instance, in all cases where a number of subspecies of a species obey one of the so-called climatic rules (of Bergmann, Gloger, Allen, etc.: see Rensch, 1939). The subspecific means then fall on a gradient, which may be called an external cline. As quantitative studies are made, interesting comparisons will become possible. Preliminary work (Huxley, 1939*b*, where other examples are also given) shows that increase of size with north latitude (Bergmann's rule) in western Europe is about three times faster in the wren (*Troglodytes troglodytes*) than in the puffin (*Fratercula arctica*).

A comparison of subspecific means, however, leaves unsolved the question whether the cline within the subspecific areas is wholly flattened out, or persists as an internal cline of very gentle slope. There are indications that in some cases at least the latter is the case (*Peromyscus polionotus*, *Parus ater*; see Huxley, 1939*b*).

Another possibility remains to be considered. It may be that existing practice in animal taxonomy has conveyed a false impression of the distinctness of subspecies and of their internal uniformity. The normal procedure is to confer a trinomial upon any form which is reasonably distinct from neighbouring types. In some cases this has been done even when it is known to be connected with other named types by continuous and gradual change; in many others the practice has been followed when neither the uniformity of the named type nor the mode of its intergradation with neighbouring types is known (examples in Huxley, 1939*a*). In such cases, clines should be employed as part of the nomenclature, either permanently, or until the existence of true subspecies has been properly demonstrated.

It would appear probable that analysis, with this question in mind, will reveal more cases of continuous slow gradation, and will also show that a large number of subspecies are not entirely uniform, but show very slight internal clines.

If so, the commonest type of partial biological discontinuity will have its profile of character change in the form of a stepped ramp, while the true staircase with flat treads, and the continuous slope, will be the less common limiting conditions at either end.

It is important also to note that clines, both internal and external, may run in different directions for different characters (examples in Huxley, 1939*b*), so that their enumeration is necessary to give even an approximate picture of the complex variability of species in nature.

There are, of course, numerous other interrelations of taxonomy and genetics, including many phenomena of what may be called consequential evolution. These are pseudo-orthogenetic limitations of evolution, dependent on the organism's mode of development, and so involve questions of physiological genetics.

In certain cases, clines should be incorporated into the nomenclature, it is suggested in the form of a hyphenated trinomial, prefixed with the abbreviation *cl* (see Huxley, 1939*a*).

But here space permits me only to touch on one further point, of quite another nature. Numerous workers have pointed out that certain types of genetic systems confer immediate advantage at the expense of long-term evolutionary success.

High autopolyploidy reduces plasticity by preventing the expression of recessive mutants; structural hybridity based on segmental interchange, as in *Oenothera*, limits the plasticity in other ways, and seems to promote immediate advantage only at the expense of ultimate extinction (Darlington, 1939).

Other workers have pointed out that the present and the immediate geological past have been productive of especially rapid organic change. For instance, the dying out of the African great lakes in the interpluvian and their subsequent filling has initiated the intensive Cichlid radiation mentioned on p. 159. The fifty-eight endemics of Victoria-Kioga have arisen from a handful of ancestral forms in perhaps 20,000 years—a geologically very brief period. This outburst of change has been brought about not only directly through rapid alterations of environment, but indirectly by causing wholesale disjunction of species into parts which were then forced to differentiate in isolation, but sometimes later allowed to meet again, and by large-scale migration and range changes. We are fortunate in living in an epoch characterized by a rare diversity of organic life as well as of scenery.

Still others have combined these two points of view. For instance, Babcock and Stebbins (1938) have shown that the present extraordinary diversification of the genus *Crepis* is due to hybridization, polyploidy, and apomixis brought about by recent range changes, but is also to be regarded as a temporary phase in evolution, since the processes at work, while affording a means of adaptation to rapid environmental change, involve a loss of evolutionary plasticity which in the long run will lead to wholesale extinction.

The same is doubtless true of many other types, notably among plants. Thus we must remember, in

considering evolutionary genetics in broad perspective, that the present condition of affairs, as represented in existing taxonomy, is in many respects exceptional.

In general, much of the organic diversification revealed by taxonomy is irrelevant to the major processes of evolution, as represented by the comparatively few broad trends of specialization and the much fewer trends of biological progress.

Some minor evolutionary processes represent detailed adaptation of a specialized form to the enormous variety of habitat that will always be present. Others, like the divergence of island populations, are still more irrelevant in being non-adaptive. Finally, still others are irrelevant temporarily rather than spatially, being temporary evolutionary devices which in the long run doom those which adopt them to extinction.

The aim of taxonomy should be to give an accurate and intelligible description of the facts of organic diversity. To do this we must call genetics to our aid. The resultant science of evolutionary genetics reveals that different types of taxonomic units and different processes of taxonomic differentiation have surprisingly different functions within the evolutionary process as a whole.

We must build up a natural history of the groups that are actually found in nature, taking account of their genetic structure, their biological properties, their evolutionary potentialities. To achieve such a science of comparative taxonomy, we need closer liaison between the great museums and general biology, and we need a large increase and diversification of museum staffs.

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135

IBSEN, H.L. and BOGART, R. *Pigmentation in Relation to Colour Inheritance in Mammals*

Hairs from cattle, guinea-pigs, horses and swine, and wool from sheep, have been examined. In all, black pigment is in the form of opaque clumps or granules. Black hairs from the above animals, in addition to containing closely packed black pigment in both the cortex and the medulla, have the intervening spaces filled with diffuse, almost transparent, red pigment. Black fibres in the wool of Hampshire sheep have only the clumped black pigment. In red hairs the cortex and medulla are filled with diffuse red pigment, with a relatively small amount of the clumped black present. The amount and the distribution of the latter determine to some extent the apparent intensity of red hairs. The chief cause for variation in shade of red hairs, however, is in the red pigment itself, which varies from a pale cream to a deep red. "Blackish" red hairs (found in Ayrshire and Jersey cattle, in bay and brown horses, and in "black tipped" (*Ti*) guinea-pigs) have more black pigment in the cortex than is found in typical red hairs. Both kinds of red hair

always have more black pigment in the medulla than in the cortex.

White hairs contain no red pigment. A few have a small number of black clumps in the cortex, but the majority have a relatively large amount of black in the medulla. The amount and the kind of pigment in the cortex (as opposed to that in the medulla) is of prime importance in determining the macroscopic appearance of any hair. White fibres from Hampshire sheep contain no pigment.

Hydrogen peroxide (strength 15 %) bleaches black pigment much more rapidly than it does red. Black hairs from cattle, horses and guinea-pigs, treated simultaneously, lose the black pigment in the cortex within 24 hr. No species difference is apparent. Red pigment shows in all of the black hairs after the black has been bleached out. The red in red hairs, as well as the red in bleached black hairs, bleaches very slowly, about three weeks being required.

Bleached black and chocolate hairs from c^rc^r ("non-red") guinea-pigs, as well as whole mounts of c^rc^rpp (pink-eyed) hairs, reveal the presence of diffuse red pigment in the cortex of both the black and the chocolate hairs. White hairs from c^rc^r animals are devoid of red pigment. From the name, one would have expected that c^rc^r animals carry no red pigment.

Dilution genes usually affect one kind of pigment more than the other. Dun in cattle and pink-eye dilution in guinea-pigs are due to a marked decrease in number of black pigment clumps, thus allowing the red to show to some extent. Different shades of red hair are due to genes acting primarily on red pigment. The same genes affect the shade of red pigment in black hairs, but this is not apparent macroscopically. One proof for this is found in the fact that when the black pigment of black hairs from a number of Hampshire hogs is bleached, the shade of the red pigment that remains varies considerably with the different individuals.

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Ives, P.T. ***A High Frequency of Lethal Mutations in a Wild Population of*** **Drosophila**

Drosophila melanogaster males were collected in October 1938 from a fruit-farming area in South Amherst, and 151 of their second chromosomes were analysed by the use of *S*/*Cy*. In the final matings of *Cy*/wild, forty-seven chromosomes proved to be lethal: i.e. less than 1 % of non-*Cy* flies appeared in a minimum of 200 flies from two or more test generations. An additional eighteen chromosomes were incompletely lethal, giving frequencies of non-*Cy* flies ranging between 2 and 17 %; and fifteen of these showed visible mutations. Twelve non-lethal chromosomes showed visible mutations, making a total of seventy-seven (51 %) which carried one or more lethal or visible mutations. Of the eighty-six chromosomes not classed as lethals, ten gave inconsistent frequencies of non-*Cy* flies, due apparently to a marked decrease in the developmental rate of non-*Cy* flies, which was sometimes lethal-like in effect in unfavourable food conditions. The remaining seventy-six chromosomes gave consistent frequencies of non-*Cy* flies ranging between 20·8 and 33·8 %, with a mean frequency of 27·63 ± 0·23 % and a mean total observation, per frequency, of 512 flies from several generations. The mean frequency is clearly below the expected 33·33 %. Only twenty-six frequencies deviated from this expectancy by less than twice their standard errors. The spread of the frequencies is broader than a normal distribution: nineteen of them deviated from the mean by more than twice their standard errors. These observations suggest the presence of deleterious genes in the majority of the seventy-six chromosomes; but the possibility of a favourable dominant genetic situation in the laboratory-bred *Cy* chromosome has not been investigated. The high lethal frequency far exceeds any frequency reported from a similarly analysed wild population of *Drosophila*. It is equalled in a less extensive analysis by Plough of a 1938 Belfast, Maine, population. It appears to be associated with a comparatively high mutation rate, and with an extreme seasonal fluctuation in population size. Data to date indicate a rate of 1·8 % per generation in 437 tests. The population size reaches a peak of probably many thousands of flies in South Amherst orchards and gardens in the early fall, and diminishes to isolated populations of only a few individuals per group in fruit and vegetable cellars during the winter. Under the latter conditions, as pointed out by Wright, the effects of natural selection are minimized and differential accumulation of mutations is favoured, while in the summer spreading of mutations may be expected as the groups intermingle. That the population does continue is indicated by the appearance of the comparatively rare mutation, "cardinal", in South Amherst collections of 1931, 1932, and 1938.

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Jaap, R.G. ***Proportional Body Shape and Growth in the Domestic Fowl***

The purpose of this study is to express body shape of the living bird in simple mathematical terms, to further the knowledge of the genetics of body conformation in the domestic fowl. Only three linear dimensions are considered sufficiently accurate for genetical research on either the domestic fowl or the

domestic turkey. When considered as ratios of the cube root of the body weight, proportional length of the tarso-metatarsal section of the leg (shank) proves to be a superior measure of general body shape. Minimum anterior body depth, when considered in the same manner, adds considerable information. Proportional length of keel or carina is the poorest measure of conformation.

Two years' observations on 1540 adult females representing six different varietal races whose environment was kept as uniform as possible revealed greater differences between the means of the varieties than between individuals within each variety. It is concluded from these records that White Wyandottes and Buff Orpingtons have proportionally greater weight for their shank length. Proportional body weight of Barred Plymouth Rocks, White Plymouth Rocks, and S.C. Rhode Island Reds is intermediate, while White Leghorns have much less weight in proportion to the length of their shanks. These differences are considered to be breed specific. While there are definite hereditary differences when body shape is expressed as proportional anterior body depth or length of keel, it appears that different strains of the same breed may differ considerably. In general, Buff Orpingtons and S.C. White Leghorns bred according to the American Standard of Perfection are proportionally deeper-bodied than the other varieties studied.

The live measurements from either growing or mature live birds may be used to predict the economic value of these fowl when prepared for human consumption. When two live birds of the same weight are compared, the one having the shorter shank and smaller body depth has the more pleasing conformation when it is prepared for the table. From the standpoint of poultry husbandry, these measurements may be used in breeding for superior table quality in egg-laying or meat strains of fowl. Comparisons between 523 cross-breds and 442 pure-bred half-brothers and half-sisters will be given as demonstration of the value of these measurements in genetical studies of body shape during growth.

The tarso-metatarsal section of the leg reaches its mature length relatively early in the growth period of the bird. For females, mature shank length is reached somewhere between 16 and 22 weeks after hatching. Relatively few females show an increase in shank length after they are 20 weeks of age. Males require approximately 4 weeks longer to reach mature shank length. Anterior body depth and keel length continue to increase during most of the growth period which, in female fowl, is approximately 40 weeks. Should the body shape of a strain be relatively uniform, length of shank may be used to predict adult body size 4–5 months prior to completion of growth.

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JAGGER, I.C. and WHITAKER, T.W. ***The Inheritance of Immunity to Mildew*** **(Bremia lactucae)** ***in Lettuce***

The production of disease-resistant plants by methods of plant breeding offers the most feasible avenue of approach in controlling some of the serious diseases of lettuce. First, brown blight, and later downy mildew have been brought under control by producing well-adapted, disease-free varieties through hybridization and selection.

The development of varieties resistant to downy mildew (*Bremia lactucae* Reg.) is complicated by the tendency of this fungus to produce (probably by mutation) distinct physiological races. A series of inoculation experiments, spread over a period of years, indicates that there are at least five physiological races of this fungus which attack cultivated lettuce.

Analysis of F_2, F_3, and backcross data of the progeny resulting from crosses between resistant and susceptible plants indicates that immunity to one of these physiological races is dependent upon a single dominant gene. The dominant genes for immunity have been found only in the more primitive types of lettuce, i.e. forms which are non-heading, quick bolting, etc. These primitive types of lettuce occur in Europe, and presumably come from near the centre of origin of cultivated lettuce.

There is no evidence of linkage between genes for immunity and any of the various morphological characters found in cultivated lettuce; consequently it is a comparatively simple matter to combine the genes for immunity with those genes which condition acceptable commercial qualities. Pedigree charts illustrating in detail the development of disease-resistant plants through hybridization and selection have been worked out.

In a consideration of the methods by which physiological races of *Bremia lactucae* may originate, it is suggested that indirect evidence points strongly to their origin through mutation.

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JANAKI, E.K. ***Triplopolyploidy and the Production of Fertile Intergeneric Hybrids in*** **Saccharum**

The formation of "diploid" gametes being a common feature in *Saccharum* the fertilization of $2n$ egg cells gives rise to triploid seedlings in both selfed and hybrid populations of the two octoploid species *S. officinarum* and *S. Spontaneum.* Unlike "diploid" hybrids, these "triplo-polyploids" are fertile and have yielded economically useful types of sugar canes.

A comparative study of the hybrids of sugar cane with *Zea Mays* and *Imperata cylindrica* and of *Saccharum Spontaneum* with *Sorghum durra* and *Ereanthus ravennae* is presented to show the underlying cytological causes for the production of fertile intergeneric hybrids in *Saccharum.* Evidence for the occurrence of diploid parthenogenesis in such triplo-polyploids is also given.

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JEFFREY, E.C. ***Apomixis in the Genus* Trillium**

Trillium has always been used as an admirable object for cytological investigations on account of the huge size of its chromosomes. This genus, which is found in North America and in Asia, presents cytological peculiarities in both continents. The descriptions of its meiotic divisions reveal extreme irregularities and a large amount of sterility. It has been supposed that these abnormalities were due to the intolerance on the part of the genus to cultivation. The present author has satisfied himself that this is not the cause of the irregularities, since they are present just as strikingly in material gathered from normal wild plants as in those under cultivation. As a result of the investigation of the processes leading to the formation of the embryo in certain species of the genus it became clear that, in contrast to the dandelions and hawkweeds (*Hieracium*), apomixis rather than parthenogenesis is present. The reduction division in the embryo-sac mother cell is quite normal in contrast to the situation in the pollen mother cells, and five chromosomes are present. One of the derivatives of the mother cell survives, as is usually the case, and gives rise to an embryo-sac. Ordinarily this contains only four nuclei, a situation paralleled by the Onagraceae and allied forms, as well as by certain orchids. Of the four nuclei one becomes the egg and the other an abortive synergid. The remaining two nuclei fuse together and form the endosperm nucleus. The pollen tubes do not usually penetrate the ovary, and in the rare cases that this happens they do not effect fertilization. There is as a consequence no fecundation of either the egg or the endosperm. In spite of the absence of fertilization, the egg develops into an abortive embryo in which the divisions show five chromosomes; in other words, the embryo is haploid. This embryo does not attain any considerable size and ultimately aborts. The endosperm, which is diploid as a result of its method of origin, forms in the usual manner and first contains a large central cavity around which are rapidly dividing cells. After the abortion of the haploid embryo and after the endosperm has reached considerable degree of development, a diploid embryo makes its appearance in the micropylar region of the endosperm, and is continuous with the endosperm tissues. This is the embryo which perpetuates the plant. Frequently with the abortion of the haploid embryo the whole seed aborts. In other cases the seeds may reach a certain size without any embryos in them at all, and in a number of instances what appear superficially to be seeds, even when relatively mature, do not contain an embryo. In certain cases all the seeds in an ovary may be in this condition. In all the mature seeds examined by the present writer in the following species of *Trillium* embryos produced from the endosperm were found to be present: *T. grandiflorum*, *T. erectum*, *T. undulatum*, and *T. sessile.*

It would appear from the abnormal method of reproduction in *Trillium* that too great an importance cannot be attached to the reproductive chromosomes of the anthers and their behaviour.

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JENKIN, T.J. ***Evolution in Wild Populations***

The two grass genera *Lolium* and *Festuca* have not been subjected to conscious selection on the part of man until quite recent years, so that practically all the material available may be regarded as "wild", even though one species, *Lolium perenne*, has been in cultivation for nearly 300 years.

L. perenne has been very extensively studied, and has been found to show quite distinct tendencies to mass divergence of type under different environmental conditions, while large populations from various sources show an infinite variation in details. The impression gained is that the species is in a very fluid condition.

Other species have not been so extensively studied, but in some of them very considerable variation in type is found.

These intraspecific variations, as a rule, are quite distinct from interspecific differences, although it is not always easy to identify specimens by means of morphological differences alone.

At least six major types of *Lolium*, classifiable as independent species, are known. Morphologically these suggest degrees of phylogenetic relationships and descent from a common prototype from which all are ultimately derived. Breeding experiments show different degrees of interspecific affinity and suggest an approximate order of derivation.

The differentiation of the *Lolium* types has not involved any change in chromosome numbers. All have remained diploids.

In the genus *Festuca* the position is very different. The genus as a whole has a wider geographical

distribution than *Lolium*, and is presumably older. It includes two main classes, the fine-leaved (Ovinae) and the broad-leaved (Bovinae) types. Interspecific crosses have been successfully made within each of these two classes, even though in each class the chromosome numbers differ. Moreover, representatives of the two classes have also been successfully intercrossed.

Thus a general phylogenetic relationship for the whole of the *Festuca* genus is indicated, although the extreme types have few morphological characters in common.

The two species, *Lolium perenne* and *Festuca pratensis*, have long been supposed to be the parents of the naturally occurring *F. loliacea*. That the two species can be successfully intercrossed has been proved, while crosses of *Lolium perenne* with other members of the Bovinae group of the genus *Festuca* have also been successful. Even more interesting, however, is the fact that *Lolium perenne* has been successfully intercrossed with members of the Ovinae group, because here there is very little morphological evidence to suggest common derivation. *L. perenne*, however, does not stand alone. The more extreme type, *L. loliaceum*, has also been successfully intercrossed with *Festuca capillata* (a diploid of the Ovinae group) and with *F. arundinacea* (a hexaploid of the Bovinae group).

If, therefore, we may assume that a degree of breeding compatibility sufficient to give rise under artificial conditions to definite caryopses, and especially to establish F_1 hybrids, is sufficient proof of phylogenetic relationship, these breeding experiments show that the two genera *Lolium* and *Festuca* are so related. Presumably, then, they are all derived from a common prototype. This common prototype probably no longer exists. It has given way to descendants which have proved to be better able to perpetuate themselves. This amounts to evolution, not only in the sense of a divergence of types with one type giving rise to another, but also in the sense that some of the successive types have a greater survival capacity than their progenitors under the existing conditions.

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JENKINS, M.T. ***The Segregation of Genes Affecting Yield of Grain in Maize***

Data reported in 1935 indicated that inbred lines of corn acquired their individuality as parents of top crosses very early in the inbreeding process and remained relatively stable thereafter. Little segregation for performance in top crosses was obtained after the second generation of selfing.

The data reported in the present paper were obtained in an effort to measure more accurately the amount of segregation for the genes affecting yield of grain in hybrids in the first generation of inbreeding, this being the generation in which it should be greatest. Pollen was collected individually from the plants in the progenies of seven different Krug plants that had been selfed for one generation and was used on the silks of twenty-five plants of the parent variety. The top crosses so obtained were compared in a yield test and the distribution of the acre yields of grain determined.

A surprisingly narrow distribution of the acre yields of these top crosses was obtained. Their standard deviation was only 2·8 bushels per acre, indicating only one chance in forty of obtaining a plant from among the siblings in these one-generation-selfed progenies so superiorly endowed that its top cross would yield 5·6 bushels or 8·9 % above the mean yield of the top crosses of all segregates.

The limited amount of segregation within lines permits, and emphasizes the importance of, early testing of the lines to determine their relative endowment with respect to factors affecting yield. It also emphasizes the possibilities of greater progress through selection among large numbers of lines rather than within lines.

A method of breeding involving the isolation of relatively large numbers of lines selfed for only one generation, the testing of these lines in hybrid combination, and the utilization of the more promising lines for the production of synthetic varieties is suggested for areas where hybrid corn may not be economically feasible. It is visualized that this would be a more or less continuous process, to be repeated after the synthetic variety had been allowed to mix thoroughly for a year or two, and possibly to be accompanied by the introduction of unrelated material.

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JENKINS, R.L. and GWIN, JANE. ***Rigorous Analysis of the Interrelations of the Frequencies of Plural Births***

By an application of Weinberg's differential rule, Dahlberg demonstrated that the frequency of dizygotic twinning is a function of maternal age, while the incidence of monozygotic twinning (in twin births per thousand births) is constant at all ages of mothers.

The development of trizygotic triplets might be expected to result from the coincident double occurrence of the process responsible for dizygotic twinning. The development of dizygotic triplets

might be expected to result from the coincident occurrence of the processes responsible for dizygotic and for monozygotic twinning. Monozygotic triplets might conceivably result from the coincident double occurrence of the process responsible for monozygotic twinning.

According to this thinking, if we let the frequency of the process responsible for dizygotic twinning be represented by a and the frequency of the process responsible for monozygotic twinning be represented by b, then the incidence of trizygotic triplets should be a^2, the incidence of dizygotic triplets should be $2ab$, and the incidence of monozygotic triplets should be b^2.

Ignoring as relatively unimportant numerically the instances in which, by our hypothesis, the processes responsible for twinning are expressed in triplet births or other plural births of higher order, we take the incidence of dizygotic twinning to approximate satisfactorily a and the incidence of monozygotic twinning to twinning to approximate satisfactorily b. Then by our hypothesis the incidence of triplet births at any age of mother $(a^2+2ab+b^2)$ should be a square of the incidence of twin births at that age $(a+b)$.

Analysis of nearly 25,000,000 births in the United States Birth Registration Area reveals that this is not the case.

However, if the incidence of triplet births at each age of mother is plotted against the square of the incidence of twin births at that age, a straight line is obtained. The equation for this line is

$$y=0{\cdot}656x+0{\cdot}00001318,$$

in which y is the incidence of triplet births and x is the square of the incidence of twin births.

Relating this to our thinking, and accepting the value 0·656 to represent the *in utero* survival rate of trizygotic and dizygotic triplets as compared with dizygotic twins, we may revise our formula for the incidence of trizygotic triplet sets to $0{\cdot}656a^2$, and that for dizygotic triplet sets to $0{\cdot}656{\cdot}2ab$. The incidence of monozygotic triplet births is not b^2 but may be represented by c, the numerical value of which is 0·0000283.

The sex distribution of triplet sets expected from this formula is in nearly exact agreement with that found.

It is apparent that since a, the frequency of the process responsible for dizygotic twinning, is a function of maternal age, the frequency of trizygotic triplets and the frequency of dizygotic triplets, being dependent on a, are also functions of maternal age. The frequency of monozygotic triplet births, is, like the frequency of monozygotic twinning, constant at all ages of mothers.

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JOHANSSON, I. ***Variations in the Manifestation of Lethal Characters in the Swedish Breeds of Cattle***

Three recessive lethal genes are known to occur in the Swedish Friesian cattle, causing the hairless, amputated, and dropsy (Larsson, 1935) conditions. The hairless calves are uniform in appearance; all specimens studied by the author agree well with those described by Mohr and Wriedt (1928). The character amputated, however, shows a wide range of variation. The author has found more extreme amputation than the case described by Wriedt and Mohr (1928), only very small external rudiments of legs being present, as well as animals with normal legs but the bulldog type of head, and calves with normal heads but legs amputated in the metacarpal-metatarsal region. There seems to be a certain correlation between the degree of leg amputation and the malformation of the head. Length of pregnancy is usually normal, irrespective of the degree of malformation. The slightly defective animals are born alive and may live for several days or weeks, but the extremely defective are stillborn or die immediately after birth. As far as can be judged from the pedigrees of amputated calves, all carry the same recessive gene, the variation in the manifestation being probably due to the modifying effect of some other genes with which the amputating gene may be associated. Some animals carrying the amputated gene may be phenotypically normal and therefore indistinguishable from non-carriers.

The congenital hydrops also shows a rather wide variation in manifestation, some foetuses being greatly enlarged through accumulation of fluid in the subcutaneous tissue and body cavities, while others are only slightly abnormal. The average length of gestation in recorded cases of hydrops is 226 days, with variation from 277 (approximately normal for the breed) to 150 days or less. Early dropsical degeneration is apparently followed by early abortion, whereas the calves may be carried to full term when the degeneration starts late. Pronounced dystocia is the rule when pregnancy lasts over 200 days. A dropsical foetus may weigh 100 kg. (normal birth weight about 40 kg.).

It seems probable that the variation in manifestation of the amputated and the dropsy characters is due to the time during foetal development when the effect of the lethal gene is unfolded. The action of the gene may be accelerated or retarded by the other constituents of the genom.

The author has found a new lethal character in native Swedish cattle, which in the cases studied have shown very little variation. Calves are born at full term and normal in every respect except that the first and second phalangeal bones are missing. The hoofs

are normal but connect with the metacarpal and metatarsal bones only by the tendons and the skin; therefore the calves cannot stand on their feet but crawl on the carpal joints and the hocks. The abnormality has appeared only among the progeny from some consanguineous matings, and is apparently caused by a recessive gene, although the cases on record are not numerous enough for a definite proof.

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JONES, D.F. ***Segmental Exchange in Somatic Cells of Maize***

Relocation of chromosome fragments in somatic mitoses is shown by paired mosaics in the endosperm of the maize seed when suitable chromosome markers are used. The loci found to be most useful for this purpose are *C*, *Pr* and *Su*, each located on a different chromosome. The first two control aleurone colour, the third differentiates between the sugary condition and normal starch in the endosperm.

In heterozygous seeds, having one of each of these dominant alleles, the removal of *C* produces a colourless spot; the removal of *Pr*, a red spot; and the removal of *Su*, a depressed translucent area that stains brown with iodine. Both *C* and *Pr* produce paired and unpaired spots. In these paired mosaics, cells adjacent to the colourless or red areas are darker than the surrounding normal cells, due to the cumulative action of the dominant colour determiners. *Pr* twin spots cannot always be identified clearly, and the *Su* gene rarely shows any cumulative effect. For the purpose of comparison, all mosaic areas showing the removal of only one of these three genes is classed as a single mosaic whether it is paired or not. In these single mosaics no distinction is made between deletions and translocations. Both are known to occur.

Paired mosaic areas are also found which show the simultaneous removal of gene markers from two different chromosomes. These double mosaics are colourless paired with red areas, colourless paired with sugary, and red paired with sugary areas. These adjacent areas are usually similar in size and outline. Mosaics of this type result from the removal of segments from non-homologous chromosomes and are due, presumably, to reciprocal translocation involving one or more strands of a multiple strand chromosome.

The number of single and double mosaics in untreated plants and from plants treated with X-rays shortly after fertilization is given in Table 1. The results show clearly that there is a more or less random exchange among all of the chromosomes in untreated as well as in treated material. The proportion of mosaics involving two marked chromosomes compared to those that involve only one marked chromosome is greatly increased by the X-ray treatment. This may be interpreted as showing that either the number of interchromosomal exchanges is increased relatively more than the number of deletions, or that translocations involving more than two chromosomes are increased over those translocations that involve only two.

Table 1. *The number and ratio of mosaics involving one and two chromosome markers*

	C	*Pr*	*C Pr*
Not treated	605	382	8
X-rayed	517	407	117
Ratio: Not treated	76	48	1
X-rayed	4·4	3·5	1
	C	*Su*	*C Su*
Not treated	605	129	2
X-rayed	517	301	52
Ratio: Not treated	303	65	1
X-rayed	9·9	5·8	1
	Pr	*Su*	*Pr Su*
Not treated	382	129	1
X-rayed	407	301	59
Ratio: Not treated	382	129	1
X-rayed	6·9	5·1	1

Translocations that involve more than two chromosomes are indicated by multiple mosaics showing three or more different tissues. Since these multiple mosaics are sometimes approximately equal in area and shape they presumably originated in one cell. They could arise from two or more translocations occurring independently in the same cell, or from more than two chromosomes exchanging at one common point of contact.

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JONES, E.T. ***A Comparison of the Segregation of Wild versus Cultivated Base in the Grain of Diploid, Tetraploid and Hexaploid Species of Oats***

The wild-base diploid species *Avena Wiestii* and *A. hirtula* and one unnamed species designated Cc 1795 were crossed with the diploid species *A. brevis* which has the cultivated type of base. *A. Wiestii* was also hybridized with *A. strigosa*, which, like *A. brevis*, has a cultivated base. In all four crosses the wild base was fully dominant in F_1. In F_2, segregation for base resulted in the production of four phenotypic groups, two like the parental forms and two new phenotypes. One of the latter has been found to breed true, but owing to the presence of a certain amount of natural crossing the true breeding character of the other has not been fully established.

In three of the four crosses there is a significant deviation in the F_2 from the expected numbers for

independent dihybrid segregation. This, it is considered, is probably due to sterility resulting from structural differences in the chromosomes and to the consequent abortion of certain gametic forms. The presence of structural differences has been demonstrated in one of the species used in these crosses by the cytological investigations carried out, and already published, by Dr W. Ellison.

Intercrossing the two new phenotypes reproduces the wild-type base.

In the tetraploid cross *A. barbata* × *A. Abyssinica* dominance of wild over cultivated base occurs in F_1. Four phenotypic groups appear in F_2 in proportions corresponding closely with a four-factor segregation. The numbers in the respective groups indicate that the factors determining wild base when in the simplex condition are dominant over the triplex condition of the recessive genes.

The hexaphoid cross, *A. fatua* × *A. sativa* (wild × cultivated base), produces an F_1 with a nearly solidified base. Segregation in F_2 is monofactorial, and, unlike the segregates in the diploids and tetraploids, the wild-type base is invariably associated with a strong, geniculate awn.

It is tentatively concluded, from the apparent reversal of dominance of base in the diploids and tetraploids on the one hand and hexaploids on the other, and the differences in the mode of segregation, (1) that the cultivated hexaploid possesses a new gene (or gene rearrangement) which differs from that determining cultivated base in the diploid and tetraploid groups. This new gene inhibits the development of the wild-type base and is linked with a gene which inhibits awn development; (2) that the monohybrid fatuoid segregation in hexaploids is not a segregation of wild- and normal-type genes acting as allelomorphic "units", but a segregation of the linked genes which inhibit the development of the awn- and the wild-type base, which genes are specific to the cultivated hexaploid oats. It is these genes which are linked and not those determining the fatuoid characters. The appearance of series A fatuoids in cultivated hexaploids is incidental to a mutational change, or deletion, in the inhibiting genes, and is due to hypostasis.

147

Jones, I. Chester. ***Red, Roan and White Coat Colour in Shorthorn Cattle***

Data obtained from the Duke of Westminster's Herd of Pedigree Dairy Shorthorns agree, for the most part, with those of other workers as regards both the "normal" results and the "exceptions". The "normal" results can best be explained by the hypothesis that all Shorthorns are homozygous for Red, the colours White, Roan or Red depending on the presence or absence of an epistatic White: Red=**RRww**; White=**RRWW**; Roan=**RRWw**. Hypostatic Red seems to be indicated in homozygous white animals by the presence of Red hairs in the fringes of the ears, and in the eyelashes. White-spotting is governed by a separate factor and may be ignored in the present discussion, Red-and-White animals being taken as Red.

A few results do not fit in with the suggested scheme:

Red × Red gave Reds or Red-and-Whites with 1 *Roan exception.*

Red × Red-and-White gave Reds or Red-and-Whites with 3 *Roan exceptions.*

Red-and-White × Roan gave Reds, Red-and-Whites and Roans with 1 *White exception.*

Similar exceptions have been found by nearly all workers in this field, and various explanations have been offered. Certain facts observed in the Duke of Westminster's Herd seem to offer an explanation of the exceptional results in keeping with the genetic scheme suggested.

Roans vary from dark "Red Roans" to almost white animals, with all gradations in between. It seems unlikely that such wide variation should not occasionally extend even farther, thus giving all-red or all-white animals; and if this happens it will account for all known exceptions. With this in mind, the anomalies in our data have been examined individually. The offspring of each show that it bred according to its registered colour; but in each case, one or the other of its parents had, from other matings, given offspring which were also exceptions. In each case the parent in question had bred as a Roan although registered as a Red or Red-and-White. It has not been possible to examine these parent animals, but it is unlikely that, where Roans are as much sought after as they are in Shorthorns, a Roan would be registered as a Red. Walther found three animals breeding as Roans, though phenotypically two were Red and one White. He used these as examples of "Transgressiv-fluktuierender Faktoren", an entirely different conception from the one here put forward, but his observations are exactly comparable to our own.

It is here suggested, then, that in Shorthorns, homozygous Red animals are **RRww**, homozygous Whites **RRWW**, and that the heterozygote **RRWw** is usually Roan, the variation in Roaning extending on rare occasions, however, to Red at one extreme and to White at the other. The data to hand do not suggest modifying factors in relation to the variation in Roaning: it appears to be a case of varying dominance depending, probably, on the whole gene balance of the organism.

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KALLMANN, F.J. ***The Scientific Goal in the Prevention of Hereditary Mental Disease and Racial Inferiority***

As it is the primary task of human genetics to determine and prevent the biological incapacity for responding favourably to contemporary standards of culture and civilization, the negative eugenic scope is narrowed to those members of all population groups who are, to a hopelessly incurable extent, either mentally defective or hereditarily insane. Of course, in leading the preventive fight against the incontrovertibly dysgenic and socially destructive tendencies of hereditary mental disease, the medical branch of human genetics cannot be satisfied with the mere accumulation of evidence as to the actual operation of predisposing genetic characters as underlying agents, nor stop at devising the most harmless sterilization methods. The real goal is the determination of the various physiological, constitutional and dispositional factors governing the phenotypical manifestation of hereditary predispositions, and the description of their structural equivalents in proper morphological terms.

In the disease group of schizophrenia, the preliminary results of our first complete series of 218 schizophrenic twin pairs and their families lend further aid to the conclusion that no genuine case of a schizophrenic psychosis is developed without the pre-existence of a specific genotype that is uniform for all the various forms of the disease. The manifestation of this genetic character is inhibited in about 20 % of the homozygotic taint-carriers by the aid of a strong constitutional resistance or by the absence of furthering dispositional factors. The significant influence of the physical structure on the onset and form of schizophrenia is indicated by corresponding differences in the manifestations of basically concordant twin psychoses and by quite consistent morphological dissimilarities in the discordant sets of twins.

As to the differences in concordance of schizophrenia between identical and non-identical twin pairs, our material yields a contrast that is even a little greater than those in Rosanoff's and Luxenburger's surveys. In forty-five out of our fifty-seven sets of monozygotic twins *both* members are affected, giving an uncorrected concordance rate of 78·9 % and a corrected probability rate of 81·7 %. The corresponding figures for all dizygotic twin pairs are 7·5 and 12·5 %.

The comparison of this expectancy figure for the non-identical twin brothers and sisters of schizophrenic twins with those for their siblings shows a striking correspondence with regard to both the total sibling rate of 12·9 % and the subgroup figures of 13·3 and 12·7 % for the respective siblings of monozygotic and dizygotic twins; while the corrected schizophrenia rate of 9·9 % for the parents of our probands is in accordance with our previous fertility statistics for schizophrenic families and supports the theory that a continuous process of selection takes place in the reproduction of new schizophrenic taint-carriers.

Comparative studies on our racially most heterogeneous material rule out any possible effect exercised on the incidence of schizophrenia by the influence of a so-called racial disposition or of intermarriage between different racial groups. There is no statistical evidence whatsoever as to consistent variations in the frequency or form of hereditary mental disease, if we compare the biological qualities of the offspring produced by intermarriages with those of the descendants of marriages contracted by parental sibships within their own respective racial groups.

149

KAUFMANN, B.P. ***Distribution of Induced Breaks along the X-chromosome of*** **Drosophila melanogaster**

An extended study, of which the preliminary results are here recorded, is being made of the distribution of X-ray-induced breaks along the *X*-chromosome of *Drosophila melanogaster*. Up to the present time the positions of approximately 600 breaks have been determined, in each case within the limits of the lettered subdivisions of Bridges's 1938 salivary chromosome map. Distribution has been determined both in chromosomes having the wild-type sequence of genes and bands, and in chromosomes carrying the *ll*-49 inversion. No significant differences occur in the distribution of breaks in these two types of chromosomes. No reinversion was observed, nor do the data show any indication of an increased frequency of breakage at the points of inversion or in regions adjacent thereto. Accordingly, general conclusions may be derived from the data as a whole. At least 2 % and probably as many as 24 % (depending on the distribution of certain questionable cases), of all observed breaks occur in the hetero-chromatic division, 20 A–F. If to the observed there is added the estimated percentage of undetected breaks which are restricted to heterochromatin, the total approaches the value of about 33 % expected on the assumption proposed by Kaufmann and Demerec that break frequency is proportional to mitotic metaphase chromosome length. Expected frequencies within the euchromatic regions have been determined on the basis of proportional length and number of bands per

subdivision of the salivary chromosome. Using these criteria, break frequency per division and subdivision conforms in general with expectancy. This is strikingly clear for the tip region (division 1 A–F) in which, according to some earlier data, break frequency showed a high value characteristic of the free ends of chromosomes. Certain subdivisions show, however, a marked increase above expected values. These regions are primarily 11 A, 12 D, 12 E, and 19 E, all characterized by irregular and disturbed pairing in the salivary gland nuclei and appearing cytologically to represent "repeats". Assuming that all observed breaks in these regions were induced by the radiation and are not attributable in part to mechanical disturbances arising from pairing within the "repeats", the possibility exists that the increased frequency indicates the presence of intercalary heterochromatic sections in the so-called euchromatic divisions of the *X*-chromosome. Certain cytological observations lend support to this interpretation.

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KAUSCHE, G.A. ***Untersuchungen zum Problem der biologischen Charakterisierung phytopathogener Virusarten***

Die Virusproteinen kommen unter den chemisch definierbaren Wirkstoffen eine besondere Stellung zu, weil sie ganz bestimmte formative Prozesse bewirken können und sich wahrscheinlich autokatalytisch vermehren. Diese Eigenschaften berechtigen dazu, nach Analogien allgemeiner und besonderer Art zwischen den Genen und Virusproteinen zu suchen. Versuche in der Richtung führen zu der Konsequenz, den Wirkungserfolg und die Wirkungsweise der Viren mit ihren physikalisch-chemischen Eigenschaften kausal zu verknüpfen. Wenn dann experimentell durch übersehbare Einflüsse die Wirkungsweise des Virus geändert werden könnte, dann müsste der veränderte Wirkungseffekt mit einer Veränderung der physikalisch-chemischen Eigenschaften gepaart gehen.

Es ist versucht worden, mit der elektronenoptischen Strukturanalyse, mit Hilfe der quantitativen Messung der Strömungsdoppelbrechnung, der nephelometrischen Ammonsulfat- und Aziditäts-trübung und der Viruseiweiss-Goldadsorption als Kolloidreaktion das Tabakmosaik- und Kartoffel-*X*-Virus nach der physikochemischen Seite hin zu charakterisieren. Die Moleküle des Tabakmosaikvirus bestehen aus *ca.* 15 mμ breiten und 330 mμ langen Stäbchen mit bestimmten Aggregations- und Adsorptions-eigenschaften, die lichtoptisch und elektronenoptisch definiert werden können.

Bei Bestrahlungen von hochgereinigtem Tabakmosaikvirus in fester Substanz oder wässerigen Lösungen mit Röntgen- oder γ-Strahlen war kein Effekt in Richtung auf eine festinduzierte Modifikation des Wirkungserfolges festzustellen. Bestrahlt man aber mit 12,000–16,000 r. oder mit 10 mg. Mesothorium grüne Blätter und verimpft den virushaltigen Pressaft über *Nicotiana glutinosa* oder *Datura stramonium* nach den Prinzipien der Selektionsmethode auf die total reagierende *N. tabacum* Samsun, dann erhält man in einem gewissen Prozentsatz der verimpften Einzelherde konstant bleibende Symptomveränderungen gegen normal. Dieser Symptomveränderung liegt eine "Mutation" der Virusmoleküle zu Grunde, die z.T. mit physikalisch-chemischen Methoden nachweisbar ist. Die Röntgen- und γ-Strahlen-"Mutanten" bleiben konstant. Chemische und physikalische Einflüsse vermögen sie nicht zu ändern. Man hat bisher den Eindruck, als ob sich die Moleküle nach zwei Richtungen geändert haben, für die eine Gruppe scheinen die Moleküle "kleiner", Achsenverhältnis 18 : 1 gegen 22: 1 normal, für die andere Gruppe "grösser", 30 : 1 gegen 22 : 1 normal geworden zu sein. Die gesteigerte Polarität der Moleküle der letzten Gruppe äussert sich in besonders stark ausgeprägter Neigung zur Bildung von linearen Aggregationen.

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KELLEY, R.B. ***Animal Industries in Tropical Australia***

The first permanent settlements in Australia were confined to the southern and south-eastern littoral, and in the rapid expansion in every practicable direction, eventually to the tropics, the settlers were limited in their choice of the breeding stock to that available in the country. As most of the settlers were from the British Isles and preferred the breeds of stock with which they were familiar, the flocks and herds of Australia are of European origin, and principally the progeny of stock imported from the British Isles. The climate is of three kinds: tropical savanna, low-latitude steppes and low-latitude desert. There is a narrow belt of rain forest upon the eastern coast, and only one effective area of 12,000 square miles on the Atherton Table-land where an altitude of approximately 2750 ft. modifies a climate typical of the latitude (17° 23′). Management is extensive; water supplies may be from surface catchments, but greater reliance is placed upon subterranean supplies which, upon occasion, are high in saline and alkali carbonates. Chief of the epizootic diseases are pleuro-pneumonia of cattle and tick fevers. Buffalo flies (*Liperosia exigia*) are present, and osteomalacia, particularly in young lactating females, occurs in

many parts. Continuous exploitation both of water and feed has reduced the natural carrying capacity. Approximately 10,000,000 sheep and 4,200,000 head of cattle are depastured under natural conditions. 62,000 cattle are dairy breeds in two principal locations on the east coast. Pigs, goats, camels, buffaloes, donkeys and mules are of minor importance. The annual gross income from animal industries is estimated to approximate £8¼ million (Australian), or about 2½*d*. per acre. All the sheep are fine-wooled merinos of the "Peppin" or "South Australian" types. They are subject to heavy losses from drought but recoveries are almost phenomenal (from 7 to 24 million in 14 years in Queensland after the 1901–2 drought). Relatively few slaughterings (5 %) take place. Among the beef cattle 82 % are of unspecified breeds (most showing Shorthorn breeding) and their crosses; in the remaining, pure-breds Shorthorns predominate (14 % of total). Herefords constitute 3 % and the remainder, viz. Red Polls, Devons and Aberdeen Angus, are fewer than 1 %. The northern killing season is relatively short, but becomes longer in the subtropical areas of Queensland. Many cattle now are brought nearer to the coast for fattening, but there is no great fattening belt as in the Argentine. On the Atherton Table-lands the annual production per cow is 64 % greater than elsewhere within the tropics, and pigs are kept in association with the dairying industry. Problems of animal production within the Australian tropics must be approached biologically and commercially. Upon ecological grounds, entire reconstruction of the animal industries may be warranted, though for many years these have returned a very appreciable gross income and so justified their maintenance. Ecological studies must be accompanied by economic investigations, and until these studies are made, animal industries within the Australian tropics should be regarded as being in formative rather than in established states.

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KEMP, T. ***The Human Chromosomes***

Winiwarter in 1912 was the first to examine the number of chromosomes in man by means of fresh tissue and modern cytological methods. The many studies on human chromosomes published since that date are critically reviewed in this paper.

The material used for these investigations consisted of germ cells and somatic cells, in normal or pathological tissue, and obtained from embryos, children, and adults, of various ages and races (Whites, Negroes, Mexicans, Indians, Japanese and Manchurians). The methods employed were: ordinary histological section, smears, *in toto* preparations of the fetal membranes, pleura, peritoneum, and tissue cultures from embryonic soma or blood cells; it has recently been shown also that sternal puncture provides a practicable method of studying human cell division.

The results attained may be classified as follows:

(1) The diploid number in ♀ is 48 (sex chromosomes *XX*) and in ♂ 47 (*XO*). This was the result obtained in 1912 by Winiwarter, who, supported by Oguma and Kihara, has maintained his opinion concerning the *XO* type of the male sex-chromosomes up to the present.

(2) The majority of the authors who have during the last two decades examined human cell division have counted 48 chromosomes diploid or 24 haploid in both sexes, finding *XX* in ♀ and *XY* in ♂ (Painter, Kemp, Evans and Swezy, Hoadley and Simons, Allen, Pratt and Newell, Minouchi and Ohta, Shiwago and Andres, Andres and Vögel, Andres and Nawaschin, King and Beams, Iriki, Schwarz). The same number was determined in *Macacus rhesus*.

(3) Several recent investigators have, however, found numbers of chromosomes in various normal human tissues that deviated essentially from 48, the diploid counts varying from 20 to 85 (e.g. Grosser, Molas, Schachow, Adamstone, Karplus, Caffier, Chrustschoff and Berlin, and Andres and Jiv). Some of these authors suppose that this variation in numbers is due to abnormal mitoses, fragmentation, elimentation, and non-disjunction; and some emphasize that all counts differing widely from 48 must be attributed to inadequate methods.

(4) Normal mitoses with 48 chromosomes are often found in pathological tissue, for example cancer tissue; on the other hand, considerable deviations from the normal number and other abnormalities are also frequent (Belling, Kemp and Heiberg, Evans and Swezy, Picon, Andres, Levine, Ludford and many others, confirming Hansemann's original observations and elucidating Boveri's well-known theory).

Some authors (Andres and Nawaschin) claim that they have been able to identify the ten largest pairs of autosomes; and numerous investigators have localized the *X*- and *Y*-chromosomes in many human dividing cells.

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KHISHIN, A.F. EL. ***The Present Conditions of Animal Breeding and Husbandry in Egypt***

The cattle, buffalo, and sheep populations of Egypt and the conditions of husbandry are briefly described, and an account is given of the activities of the University Faculty of Agriculture, Giza, with cattle and poultry importations towards the encouragement of livestock improvement.

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KNAPP, E. und SCHREIBER, H. ***Quantitative Analyse der mutationsauslösenden Wirkung monochromatischen U.-V.-Lichtes in Spermatozoiden von*** **Sphaerocarpus**

Die besondere Bedeutung einer experimentellen Erforschung der Mutationsauslösung durch nicht-ionisierende sichtbare und unsichtbare Lichtstrahlen gegenüber der Analyse der Mutationsauslösung durch die ionisierenden Röntgenstrahlen beruht auf dem grundverschiedenen Wirkungsmechanismus der beiden Strahlenarten. Während bei den Röntgenstrahlen, wie auch bei anderen ionisierenden Strahlungen, der wirksame Treffer die durch ein Sekundärelektron verursachte Ionisation oder Anregung im strahlenempfindlichen Bereich ist, wird bei der nicht-ionisierenden Lichtstrahlung der wirksame Treffer durch die direkte Absorption eines Energiequants im strahlenempfindlichen Bereich dargestellt. Da zwischen dem Bau der absorbierenden Substanz und der Energie des absorbierten Quants, d.h. der Wellenlänge des absorbierten Lichtes, direkte Beziehungen bestehen, muss auch die mutationsauslösende Wirkung der Lichtstrahlen in hohem Masse wellenlängenabhängig sein.

Die Untersuchungen verschiedener Autoren haben ergeben, dass kurzwelliges U.V. mutationsauslösend wirkt, und vor allem durch Untersuchungen von Stadler und Sprague an *Zea Mays* und von Stubbe und Noethling an *Antirrhinum* ist weiterhin die Wellenlängenabhängigkeit der Mutationsauslösung in diesem Spektralbereich gezeigt worden. Wir haben uns nun die Aufgabe gestellt, durch die möglichst exakte Feststellung der Häufigkeit der durch einzelne Wellenlängen ausgelösten Mutationen, d.h. durch die Feststellung von "Wirkungsspektren", Beiträge zu liefern zur Frage nach der Natur der genetisch bedeutsamen Substanzen in den Chromosomen. Über die bisher vorliegenden Ergebnisse dieser Untersuchungen sei im folgenden kurz berichtet.

Die erste Voraussetzung für diese Untersuchungen war, die Bestrahlungen bei einem Objekt durchzuführen, bei dem nicht ein wesentlicher, im einzelnen aber nicht genau bekannter Betrag der eingestrahlten Energie vor Erreichen des Kernes von vorgelagerten Geweben oder Zellbestandteilen absorbiert wird. Schon bei Bestrahlung von Pollenkörnern ist mit einer wesentlichen U.V.-Absorption durch die Exine, eventuell auch durch das Plasma zu rechnen. Wir haben deshalb für unsere Untersuchungen das Lebermoos *Sphaerocarpus* gewählt und frei im Wasser schwimmende Spermatozoiden bestrahlt. Diese bestehen ja praktisch nur aus Kernsubstanz, und eine vorherige, ins Gewicht fallende Absorption der eingestrahlten Energie kommt nicht in betracht. Die Bestrahlung erfolgte hinter einem Quarzmonochromator mit dem Linienspektrum einer Quecksilberlampe, und zwar mit gleichen Dosen (200 000 erg/cm.²) der Linien 254, 265, 280, 297, 302 und 313 mμ. Mit den bestrahlten Spermatozoid-Aufschwemmungen wurden normale weibliche Pflanzen befruchtet, die daraus sich entwickelnden Sporogone aufgezogen und geerntet und die in den Sporogonen gebildeten Sporentetraden ausgesät. Eine einfach mendelnde Mutation, die in einem Spermatozoid erfolgte, musste sich dadurch geltend machen, dass in jeder Sporentetrade des betreffenden Sporogons zwei Sporen normale und zwei mutante Pflanzen ergaben. Letale Mutationen verraten sich dadurch, dass jede Tetrade nur zwei lebende Keime liefert. In Tabelle 1 sind in der dritten Spalte die Gesamt-Häufigkeiten der auf diese Weise nachgewiesenen einfach mendelnden Mutationen für die sechs geprüften Wellenlängen und eine unbestrahlte Kontrolle eingetragen und in Beziehung gesetzt zur Zahl der analysierten Sporogone. In der vierten Spalte dieser Tabelle ist die Häufigkeit der nachgewiesenen Mutationen auf 100 analysierte Sporogone bezogen, um für den einzelnen Versuch vergleichbare Werte zu bekommen. Es ergibt sich ein Maximum der mutationsauslösenden Wirkung bei 265 mμ und ein Abfall nach beiden Seiten des Spektrums. Gleichzeitig haben wir auch die Beeinflussung des Sporogonansatzes durch Bestrahlung der Spermatozoiden geprüft. In Spalte 2 ist der Quotient aus der Anzahl

Tabelle 1

Wellenlänge mμ	Beeinflussung des Sporogonansatzes: Sporog. i. d. Vers. / Sporog. i. d. Kontr. = %	Häufigkeit der Mutationen: Nachgewies. Mutationen / Analysierte Sporogone	Häufigkeit der Mutationen, bezogen auf 100 analysierte Sporogone
254	$\frac{57}{23}\frac{75}{28}\frac{53}{35}$ = 25·5	$\frac{17}{61}$	28
265	$\frac{26}{45}\frac{58}{26}$ = 5·7	$\frac{22}{53}$	42
280	$\frac{31}{32}\frac{12}{60}\frac{2}{9}$ = 9·54	$\frac{14}{64}$	22
297	$\frac{1}{5}\frac{0}{2}\frac{2}{3}\frac{8}{3}$ = 111·4	$\frac{3}{52}$	5·8
302	$\frac{1}{10}\frac{2}{4}\frac{2}{3}\frac{3}{3}$ = 118	$\frac{4}{71}$	5·6
313	$\frac{13}{11}\frac{22}{35}\frac{3}{5}$ = 116·5	$\frac{0}{65}$	0
Kontr.		$\frac{0}{64}$	0

der in den einzelnen Versuchen und in der jeweils zugehörigen Kontrolle gebildeten Sporogone wiedergegeben und in % ausgedrückt. Auch für die Verminderung des Sporogonansatzes durch Bestrahlung der Spermatozoiden ergibt sich ein Maximum der Wirkung bis 265 mμ. Für die Wellenlängen 297, 302 und 313 ergab sich sogar eine leichte Förderung, die aber wohl nicht gesichert ist.

Das Maximum der mutationsauslösenden Wirkung wie auch das Maximum der Verminderung des Sporogonansatzes stimmt recht gut überein mit dem Maximum der Absorptionskurve der Thymonukleinsäure, wie es von Caspersson festgestellt wurde. In Fig. 1 haben wir die Absorptionskurve der Thymo-

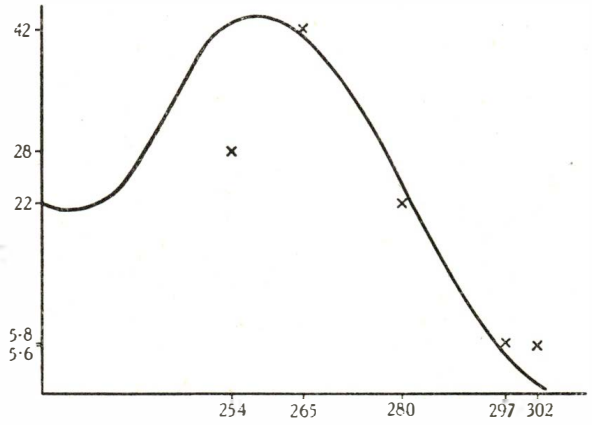

Fig. 1.

nukleinsäure nach Caspersson wiedergegeben und gleichzeitig, bei frei gewähltem Massstab, für die sechs untersuchten Wellenlängen die Häufigkeiten der festgestellten Mutationen eingetragen. Wir glauben aus den Befunden schliessen zu dürfen, dass der Absorption durch die Thymonukleinsäure wesentliche Bedeutung bei der mutationsauslösenden Wirkung des U.V. zukommt. Die Tatsache, dass die beiden Maxima leicht gegeneinander verschoben zu sein scheinen und insbesondere bei 254 mμ die mutations auslösende Wirkung schon wesentlich geringer geworden ist, dürfte auf sekundäre Ursachen zurückzuführen sein. Etwa in betracht kommende Eiweisskörper zeigen kein Maximum in dem Gebiet um 260 mμ.

Wenn unsere Untersuchungen das Vorliegen einer energetischen Beziehung zwischen der Thymonukleinsäure und der eigentlichen genetischen Substanz sehr wahrscheinlich gemacht haben, so ergibt sich weiter die Frage nach der Art dieser Beziehung. Hierfür kommen verschiedene Möglichkeiten in betracht. Jedenfalls erscheint es uns noch keineswegs als erwiesen, dass die Thymonukleinsäure selbst direkt am Aufbau der "Gene" beteiligt ist.

Wenn unsere Versuche eine so wesentliche Bedeutung der U.V.-Absorption durch die Thymonukleinsäure für die Mutationsauslösung nahelegen, so erhebt sich die Frage, ob *nur* die Absorption durch die Thymonukleinsäure zur Mutationsauslösung führt, oder ob auch die Absorption durch andere, am Aufbau der Chromosomen oder der Gene beteiligte Substanzen Mutationen auszulösen vermag. Da die Absorption von U.V. durch Thymonukleinsäure viel stärker ist als etwa die durch Eiweisse, besteht durchaus die Möglichkeit, dass die von Eiweissen absorbierte Energie ebenso mutationsauslösend wirkt wie die von der Thymonukleinsäure absorbierte, dass die durch die Eiweissabsorption bedingte Komponente des Wirkungsspektrums aber gegenüber der durch die Thymonukleinsäure-Absorption bedingten Komponente nicht ins Gewicht fällt. Es müssten, um diese Frage zu entscheiden, noch Wellenlängen herangezogen werden, bei denen die Thymonukleinsäure-Absorption gering die Absorption durch andere Komponenten, etwa Eiweisse, aber beträchtlich ist.

Wir haben unserer Auswertung die Gesamtheit der mendelnden Mutationen zu Grunde gelegt. Es fragt sich, o b wir berechtigt sind, für die verschiedenen Mutationen ein identisches Wirkungsspektrum anzunehmen oder ob nicht etwa die einzelnen "Gene", entsprechend ihrem verschiedenen chemischen Aufbau, ihr Mutationsmaximum bei ganz verschiedenen Wellenlängen zeigen. Manche Forscher haben ja, auf dieser Annahme fussend, geglaubt, durch Bestrahlung mit verschiedenen Wellenlängen qualitativ verschiedene Mutationen auslösen zu können. Nachdem wir die Absorption durch die Thymonukleinsäure in dem von uns untersuchten Strahlenbereich als wesentliche Ursache der mutationsauslösenden Wirkung des U.V. erkannt zu haben glauben, glauben wir nicht, dass sich in diesem Strahlenbereich für die Mutationen der einzelnen Gene wesentliche Unterschiede ergeben werden. Denn die Thymonukleinsäurekomponente dürfte doch wohl für alle Gene dieselbe Rolle spielen. Wenn es gelingt, die Thymonukleinsäure-Komponente bei der Mutationsauslösung auszuschalten, wäre die Frage nach qualitativen Unterschieden in der Mutationsauslösung durch verschiedene Wellenlängen des U.V. erneut zu prüfen.

Eine andere Frage ist die, ob sich für Chromosomen-Mutationen und für echte Genmutationen gleiche Wirkungsspektren ergeben. Diese Frage ist von besonderer Bedeutung für das Problem der Chromosomen-Mutationen überhaupt und deren Beziehungen zu den echten Genmutationen. Da wir nicht entscheiden können, ob und wieweit an unseren Mutationen Chromosomen-Mutationen beteiligt sind, können wir zu dieser Frage nicht Stellung nehmen.

Für die Abfassung dieses Berichtes ist der erstgenannte der beiden Autoren verantwortlich.

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KOBOZIEFF, N. et POMRIASKINSKY-KOBOZIEFF, N.A. ***Nouvelles recherches sur le mode de transmission héréditaire des anomalies des oreilles chez la Souris: abaissement avec inversion du pavillon et pavillon tronqué***

Les anomalies du pavillon de l'oreille paraissent extrêmement rares chez la souris.

En effet, on ne connaît que deux mutations de ce genre: (1) L'une d'origine américaine, connue sous le nom *short-eared* (oreille courte), consiste en un simple

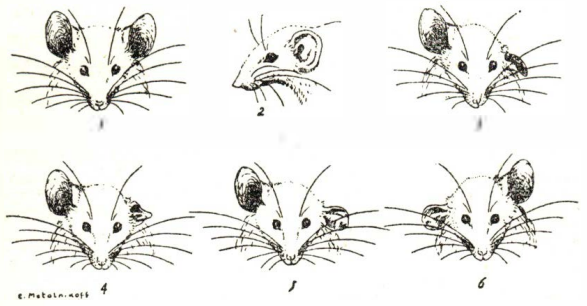

Fig. (1) Souris normale (♀ 62951). (2) Souris à oreilles courtes de C. J. Lynch. (3) ♂ 62389, abaissement avec inversion du pavillon de l'oreille gauche de 180°. (4) ♂ 62740 (fils du ♂ 62389), pavillon de l'oreille gauche tronqué. (5) ♂ 62950, abaissement du pavillon de l'oreille gauche de 90°. (6) ♀ 63363, abaissement du pavillon de l'oreille droite de 90°.

raccourcissement du pavillon, qui donne, en outre, l'impression d'être appliqué contre la crâne. Cette mutation, paraît bilatèrale. Il s'agit d'une mutation recessive, simple (Lynch, 1921). (2) La seconde, d'origine française, connue sous le nom: "abaissement avec *inversion du pavillon* et *pavillon tronqué*", caracterisée tantôt par l'abaissement du pavillon de l'oreille de 90° et 180°, tantôt par la troncature plus ou moins accusée de celui-ci; le plus souvent l'anomalie est unilatérale. Il s'agit également, dans ce dernier cas, d'une mutation recessive (Kobozieff et Pomriaskinsky-Kobozieff, 1937).

Au point où en est notre analyse génétique de cette dernière mutation, nous constatons qu'elle est recessive (exp. I, en F_1 absence d'anormaux). En admettant qu'elle est régie par un seul gène, la récessivité est d'ailleurs incomplète, car en *Fb* (rétrocroisement exp. 2), F_2 (exp. 3), F_3 (exp. 4), F_4 (exp. 5) et dans la descendance issue des deux progéniteurs anormaux (exp. 6), nous constatons un déficit notable de descendants anormaux (5·1, 2·4, 1·8, 0 et 23·6 % respectivement).

Nous supposons que ce déficit (récessivité incomplète) est dû à l'existence, dans la descendance normale, de sujets "*normal overlaps*", c'est-à-dire d'individus homozygotes recessifs mutés qui ne manifestent pas phénotypiquement leur anomalie.

Nous avons apporté, croyons nous, une preuve certaine de l'existence de ces "*normal overlaps*": (1) parmi les descendants *Fb* normaux (*FbN* de l'exp. 2), (2) parmi les descendants normaux de ceux-ci (F_2N de l'exp. 8), (3) parmi les descendants normaux issus de deux progéniteurs anormaux (F_1N_{ov} de l'exp. 6), et (4) enfin parmi les descendants normaux de deux générations consécutives (F_2N_{ov} de l'exp. 11 et F_3N_{ov} de l'exp. 12).

En effet, ces progéniteurs normaux mentionnés ci-dessus, croisés entre eux ou avec des progéniteurs anormaux, accusent une fréquence d'apparition de descendants anormaux nettement plus elevée (exps. 7–14) que dans la descendance des progéniteurs utilisés dans les expériences 2–5, ce qui indique la présence, parmi ces progeniteurs normaux de sujets *normal-overlaps*.

No. de l'exp.	Parents	Génération	% de descendants à pavillon anormal
1	Anormal × normal	F_1	0
2	Anormal × F_1 normal (du 1)	*Fb*	5·1
3	F_1 normal (du 1) × F_1 normal (du 1)	F_2	2·4
4	F_2 normal (du 3) × F_2 normal (du 3)	F_3	1·8
5	F_3 normal (du 4) × F_3 normal (du 4)	F_4	0
6	Anormal × anormal	—	23·6
7	Anormal × *Fb* normal (du 2)	*Fb*	13·2
8	*Fb* normal (du 2) × *Fb* normal (du 2)	F_2	11·0
9	F_2 normal (du 8) × F_2 normal (du 8)	F_3	7·2
10	Anormal × F_1 normal overlaps (du 6)	*Fb*	12·9
11	F_1 normal overlaps (du 6) × F_1 normal overlaps (du 6)	F_2	12·3
12	F_2 normal overlaps (du 11) × F_2 normal overlaps (du 11)	F_3	13·3
13	F_3 normal overlaps (du 12) × F_3 normal overlaps (du 12)	F_4	21·4
14	Anormal × F_2N (du 8)	*Fb*	21·5
15	Anormal × F_2N (du 3)	*Fb*	0

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KOLLER, P.C. *Crossing-over in the Sex Chromosomes of Mammals*

The analysis of various types of sex chromosomes in different organisms shows that they form an unequal bivalent during meiosis, i.e. that the sex bivalent is composed of a differential and pairing segment. The important factor which determines the meiotic behaviour of these chromosomes is the position of the pairing and differential segments in relation to the centromere. The separation of the sexes is permanently maintained because that segment of the sex chromosome, which contains the sex-differentiating gene or group of genes, is excluded from recombination; however, the pairing segments of the *X* and *Y* are homologous (internal or genic homology being the primary condition of chromosome pairing), hence chiasmata, representing genetical crossing-over, can be formed in these segments. Genes localized in the pairing segment necessarily exhibit crossing-over with the sex factor or factors localized in the differential segment. The amount of partial sex linkage of a gene may be taken as a measurement of the distance between its locus and the proximal end of the differential segment.

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KÖRÖSY, K. DE. *Outlines of a Theory of Interference*

The hypothesis of interference was introduced to explain the discrepancies between the observed frequencies of double crossing-over and those expected on pure chance. It is demonstrated experimentally that every break suppresses a certain fraction of the frequency with which every second break would have appeared without interference. In carrying this idea further the author was led to the concepts of primary recombination value (f), primary map distance (M) and strength of interference (i). The influence of distance on the value of interference can be eliminated by calculating the specific interference for the unit of map distance: $iM = I$. The theory of interference means the laws which represent I irrespective of the topographic location of the two intervals in the chromosome segments—as a simple function of M.

If two breaks lie on the same segment, the normal interference has a constant value. The normal transitive interference is independent of the distance of the first break from the boundary of the segment, but shows linear decrease with the second break from the boundary. The mirror-like form of the two transitive interferences *lm* and *mr* (*lm* = left-middle segments of *X* of *Drosophila melanogaster*, *mr* = the middle and right segments) suggests that interference starts simultaneously at both ends of the chromosome.

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KREYBERG, L. *The Relationship between "Brown Degeneration" of the Adrenals and Breast Cancer in Mice*

First is presented a short review of the most important contributions to the study of the internal cortical zone of the adrenals in mice, the zona reticularis or the "*x*-zone", with special reference to its behaviour in relation to tumour formation. The observations and theories of Cramer and Horning are cited, and the present paper is a report upon a study of a series of inbred, tar-painted and partly folliculin-injected mice, where the main problem has been to examine the so-called "brown degeneration" in relation to spontaneous and induced breast cancer. A homozygous "breast cancer" line, a homozygous "non-breast cancer" line, a heterozygous series of "early generations", as well as a series of animals designated "irregular" lines (because of the irregular occurrence of breast cancer), have been examined, in all eighty-seven animals. The brown degeneration has been graded and the main findings tabulated.

We find no significant difference in the incidence of brown degeneration in the two homozygous lines, one a practically 100 % breast cancer line, the other with only one instance of spontaneous breast cancer out of 481 females in twenty-three generations.

If the material is divided in two groups, one comprising the females with an actual manifestation of breast cancer (thirty-four animals), and another not showing this tumour (fifty-three animals), we find no difference in the occurrence of brown degeneration.

In the animals grouped according to the occurrence of brown degeneration and season ("summer", April–September; "winter", October–March), the ratio of animals showing and not showing brown degeneration is 5 : 10 and 9 : 10.

The age of the animals is not a fundamental factor in the genesis of brown degeneration. But in the animals showing brown degeneration there is a certain tendency to manifest the more marked changes with advancing age.

Six females, mated but probably sterile, developed no brown degeneration in five instances, and a low-grade degeneration in the sixth.

An examination and a comparison of the four experimental groups *inter se*, and the evidence from the literature, seem to indicate that the occurrence of brown degeneration is determined by genetic factors.

The brown degeneration cannot, as suggested by Cramer and Horning, be regarded as the "visible manifestation of the vague term 'susceptibility to mammary cancer'". It cannot be denied, but it has not yet been proved, that brown degeneration is the "visible manifestation of an adequate hormonal stimulus to breast cancer development".

The treatment of mice with oestrogenic hormones greatly favours the process leading up to brown degeneration.

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KRÜGER, L. ***Die Bestimmung von Leistungswert, Erbwert, Erbanlagen und Erbquanten bei der Milchleistung***

Die Leistungsprüfungen stellen Leistungen fest. Die Leistungen hängen vom Tier und von dessen Umweltbedingungen ab. Für die Zuchtwahl und für die Bestimmung des Erbganges sind darum Leistungen schlecht zu gebrauchen. Dazu braucht man Leistungen, die von allen Tieren unter gleichen Bedingungen (Einheitsumwelt) erzeugt wurden. *Der Leistungswert ist die Leistung bei Einheitsumwelt.* Die Einheitsumwelt kann international für Alter, Dauer der laufenden und vorhergehenden Zwischenkalbezeit und Trockenzeit festgelegt, und für Fütterung und Haltung den landesüblichen Verhältnissen angepasst werden. Man erhält den Leistungswert aus den Leistungen durch *Umwertung mit Hilfe von Vergleichszahlen.* Diese können bei Alter, Zwischenkalbezeit und Trockenzeit für ein ganzes Rassengebiet einheitlich und einmalig festgelegt werden (Erfahrungszahlen, Messtafeln). Die Wirkungen der Aussenwelt werden durch Vergleich von Monatsgruppen vereinheitlicht. Die Umwertung der Leistungen auf Einheitsumwelt erhöht die Genauigkeit um das 2–3fache.

Der *Erbwert* wird am besten durch Vergleich der Leistungswerte der Kinder mit den Leistungswerten der Eltern festgestellt. Das Erbgitter ist dazu besonders gut geeignet. Weniger erfolgreich ist eine Erbwertbestimmung durch Vergleich der Kinder mit anderen Tiermassen (Herde, Genossenschaft, Familie, Nachkommenschaft anderer Eltern, usw.).

Die Erkennung einzelner *Erbanlagen*, welche die Milchleistung entscheidend bestimmen, ist z.Z. noch nicht möglich. Die Bestimmung von Erbanlagen und vom Erbgang dieser Anlagen bleibt zunächst ein Wunschbild. Die Erfahrung lehrt, dass die Milchleistung so vielfach erblich bedingt ist, dass *ein von wenigen Erbanlagen wesentlich bestimmter Erbgang nicht in Frage kommen kann.* Dasselbe gilt auch für andere Mengenleistungen (physiologische Leistungen). Untersuchungen des Berichterstatters in vielen alten Stammzuchten haben ergeben, dass das gleiche Material, gleichzeitig und mit gleich gutem Erfolg sowohl nach der Annahme (Hypothese) von zwei Hauptfaktoren, als auch nach der Annahme von drei, vier oder fünf Hauptfaktoren bearbeitet werden kann.

Die gebildeten fünf, bzw. sieben, neun oder elf Klassen sind also *nicht ein Ausdruck von Erbeinheiten* (Erbfaktoren) wie bisher angenommen wurde, sondern Ausdruck von Erbanlagenmassen, die ich mit *Erbquanten* bezeichnen möchte. Die Erbquanten haben praktische Bedeutung für die Kennzeichnung des Erbwertes, für den Vergleich der Erbwerte untereinander und für die Voraussage der Nachkommenbeschaffenheit. Die Arbeiten mit dem Ziel, die erbliche Veranlagung und den Erbgang zu erforschen, sollten sich von vorneherein auf die vielfache erbliche Bedingtheit der Milchleistung einstellen.

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LAMM, R. ***Varying Cytological Behaviour in Reciprocal* Solanum *Crosses***

1. The pentaploid *Solanum curtilobum* can be easily crossed with the tetraploid *S. tuberosum*, whereby fertile hybrids with intermediate chromosome numbers arise.

The reciprocal crossing is difficult to perform, but it was successfully carried out by grafting the mother plant *S. tuberosum* on tomato. The hybrids produced, which also have intermediate chromosome numbers, are totally sterile.

2. Meiosis in hybrids of *S. curtilobum* × *S. tuberosum* takes place normally and in the same manner as in the parent species. Meiosis in hybrids of *S. tuberosum* × *S. curtilobum* is characterized by weak pairing during prophase, but during metaphase only univalents occur, which often arrange themselves in a regular plate, divide and pass to both poles. This gives rise to dyads, the nuclei of which, however, generally degenerate.

3. This dissimilar chromosome mechanism in these *Solanum* hybrids after reciprocal crossings may be due either to cytoplasmatic inheritance or to maternal effects.

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LAMPRECHT, H. ***The Limit between* Phaseolus vulgaris *and* Ph. multiflorus *from the Genetical Point of View***

Phaseolus vulgaris and *Ph. multiflorus* may be considered as two well-characterized Linnean species. They show distinct taxonomic differences and their hybrids are highly sterile.

As taxonomic differences the following may be cited:

Part of the plant	*Phaseolus vulgaris*	*Phaseolus multiflorus*
Cotyledons	Epigeic	Hypogeic
Inflorescence	2–5 nodes; first node about twice as long as the second	10–16 nodes; first node 3–5 times longer than the second
Flowers	Without genes for red colour	With genes for red colour, even in white flowers
Stigma	Descendent on the outside of the pistil	Descendent on the inside of the pistil
Pods	Not grooved	Transversally grooved
Seeds	No colour localization at the side of the hilum	Colour localization on both sides of the hilum

Both species have 11 chromosomes of a very similar form.

Since 1927 twenty-nine crosses between different cultivated varieties of *vulgaris* and *multiflorus* have been studied. The crosses succeeded only with *vulgaris* as ♀. The F_1 of all crosses showed about the same properties. They were composed of two types of plants: (1) large, normal green plants, *giants* (3–5 m. tall), with many hundreds of flowers and low fertility; (2) *dwarfs* with some yellowish greyish green leaves, almost exclusively with small buds and completely sterile. The proportion between giants and dwarfs varies in the different crosses—in relation to the parent lines—from 0 to 50 %.

The degree of sterility was determined by pollen investigation and seed production. The pollen of the giants consisted of 75–90 % small, empty grains and 10–25 % apparently normal grains. The seed production, however, was much lower, at most 1·5 %. Thus, if the sterility of the females was not much less than the percentage of "normal" pollen grains, a great part of these grains may have been unfit. The dwarfs usually developed only very small buds. A small number of larger buds with pollen grains was found; in these cases the pollen presented about the same picture as in the giants.

From F_{5-9} (about 20,000 plants each year) quite fertile and constant families and lines could be selected. Some lines of this kind are obtained even earlier from spontaneous crosses. These lines show either combinations of the taxonomic characters from both parent species (practically all combinations were obtained)—they may be called *Ph. multigaris*—or they are apparently like *vulgaris* or *multiflorus*. The latter may be called *neovulgaris* and *neomultiflorus* respectively.

Of particular interest were the results from crosses between *multigaris*, *neovulgaris* and *vulgaris* respectively. Thus one and the same *multigaris* line, crossed with different *vulgaris* lines, has in F_1 given the following results: (1) 100 % apparently normal plants (six crosses); (2) 90 % apparently normal plants and 10 % sterile dwarfs (one cross); (3) 100 % low, quite sterile dwarfs (two crosses); and (4) 100 % lethal plants; the latter seemed to be normal at the beginning of their development, but after 4–6 weeks all died (two crosses, of which one was studied for 3 years). The "normal" plants were always more or less sterile (70–90 %). F_1 of crosses between other lines of *multigaris*, *neovulgaris* and *vulgaris* showed similar results. The sterility varies between 0 and 90 %. All lines so far investigated showed the same chromosome number as the parents, 11.

Conclusions. The difference between *Ph. vulgaris* and *multiflorus* is caused by a number of genes (not by dominance or recessiveness in genes), which on their part are the condition for unequal chromosomal structure. In these two species the difference is not so great as to preclude the possibility of obtaining cross-descendants and—if working with large cross-populations—gradually quite fertile lines, which either represent new combinations of the taxonomic characters of the parents, as in *Ph. multigaris*, or agree with them, as in *neovulgaris* and *neomultiflorus*. It would appear that the degree of differences in the genetic constitution is the origin of corresponding differences in the chromosomal structure, and that this may be regarded as the expression of a relationship between different species. Species differences always seem to be related to chromosomal structure. But the basis is the totality of the genes, the sum of these molecular units of heredity; they also determine the morphology and behaviour of the chromosomes.

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LAMY, R. and MULLER, H.J. ***Evidence of the Non-genetic Nature of the Lethal Effect of Radiation of*** **Drosophila** ***Embryos***

In order to test whether the lethal effect of X-rays upon embryos (of *Drosophila*) is genetic or "physiological" in nature, fertilized eggs (embryos) from triploid mothers were used for treatment. If the lethal effect of X-rays were genetic, the triploid embryos would be expected to show a higher resistance than the diploids, and there would in consequence be a larger proportion of triploids among the survivors in the treated than in the control series. After preliminary tests the experiment was done three times with approximately 3000 eggs in each series, and in no case was there a significant departure in the proportion of triploids to diploids obtained in the treated as compared with the control series. It was

therefore concluded that the lethal effect of X-rays on embryos must be of some "physiological" nature.

It was also found that the order in which triploid females, diploid females, and males, respectively, from irradiated larvae showed different degrees of expression of morphological abnormalities differed in the case of different abnormalities, instead of always showing the sequence triploid females > diploid females > males, as would be expected for the expression of genetic changes. It was therefore concluded that these disturbances of development also had their seat in alterations of physiological reactions that were not caused by genetic changes.

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LANDAUER, W. ***Teratological Correlations and the Mechanism of Gene Expression***

The proportions of different body parts, though they may vary greatly in successive stages, are a remarkably constant feature in individuals of the same sex and age within one species or race. This fixity of proportions is illustrated most impressively by the high degree of correlation generally found for skeletal dimensions.

Among the deviations from normal conformation, those are of special interest which recur in a similar fashion among widely different forms of animals. For such cases are likely to reflect the effects of an interference with the fundamental mechanisms which are involved in bringing about the fixed proportionality of parts, typical of the particular species. Disproportionate dwarfism is such an abnormality. Its occurrence is widespread among birds and mammals.

It is proposed to review briefly some of the more important facts which have come to light in a study of disproportionate dwarfism of fowl, and to discuss the meaning of these facts in the light of other observations. On the whole, we shall limit ourselves to vertebrate material, although much evidence with a direct bearing on our subject is available from invertebrates.

In experiments with Creeper chickens we have reached the following conclusions which are pertinent to the present discussion: (1) In heterozygotes the principal effect of the Creeper mutation is a shortening of the long bones of the extremities (Landauer, 1934). In homozygotes, if they survive the early lethal period, both the head and the extremities are involved. In the extremities, however, the reduction in length extends to the toes (Landauer, 1933, 1939*b*). (2) The shortening of the various long bones is not uniform. Absolute reduction in length is the greater the later in normal development a bone is laid down, and, in terms of total shortening within the axis of one extremity, reduction in length is the more marked the greater is, in normal embryos, the length of the particular bone at the end of development. These rules hold for heterozygous and homozygous Creeper embryos (Landauer, 1934, 1939*b*). (3) All available evidence indicates that the peculiarities of Creeper embryos (shortening of long bones in heterozygotes; rudimentary extremities and abnormalities of skull and eyes in homozygotes) are preceded in early stages by a developmental retardation of the embryo as a whole. If the abnormalities of homozygous Creeper embryos are traced back to progressively earlier stages, it is found that a difference in embryo size is the first distinguishable feature (Landauer, 1932). After the appearance of abnormalities, there is a greater degree of reduction in size of various parts than in their histological differentiation. Limb buds of genetically normal embryos grown *in vitro* under growth-retarding culture conditions show features typical of homozygous Creeper embryos (Fell and Landauer). In tissue culture experiments, explants from homozygous Creeper and from retarded non-Creeper embryos behave in a similar fashion (David). (4) Early homozygous Creeper embryos as a rule exhibit an asymmetry of size and structure of the two eyes, the left one generally being much smaller and more retarded in development than the right. A similar situation obtains with regard to the otocysts (Rudnick and Hamburger). The head region of normal embryos shows during these stages a higher growth rate on the left than on the right side (Olsen and Byerly).

An independent mutation, with a phenotypical expression very similar to that of Creepers, has been found in Dark Cornish fowl (Landauer, 1935). As in Creeper chickens, heterozygotes have shortened long bones, while in homozygotes the extremities are rudimentary and the head is deformed. Also, as in Creepers, the toes are not involved in heterozygotes, but are shortened in homozygotes. Reduction in length of the long bones of Cornish lethal embryos is influenced by the same developmental agencies as in Creepers, viz. the sequence of embryonic origin of the bones and their inherent normal growth capacity. In the Cornish lethal, contrary to the Creeper lethal, shortening of the long bones is *not* preceded by a weight reduction of the embryo as a whole.

Another feature which Creeper and Cornish lethal embryos have in common is an enlargement of spleen and heart. There is evidence that we are dealing in this respect with a compensatory hypertrophy, brought on by lack of bone marrow and consequent anaemia. Here we have an illustration of clearly secondary abnormalities, while the co-existing malformations of head and extremities in the two types

of lethal embryos apparently trace back to general factors common to the embryo as a whole.

We have recently found a recessive lethal mutation of fowl which causes a shortening of the upper beak and a reduction in length of the tarsometatarsus. Another new lethal mutation causes head abnormalities and excessive polydactyly (Cole). No detailed information is available as yet about these mutations, but it is surely not coincidence that out of six lethal mutations of fowl, for which the morphological effect is known, four produce simultaneous abnormalities of head and extremities.

From these genetically controlled teratological syndromes we turn briefly to complex malformations which are produced by non-genetic agencies. Franke and his associates at the South Dakota Agricultural Experiment Station found that, if laying hens are fed a ration containing traces (about ten parts per million) of naturally occurring selenium, no chicks will hatch from any of the eggs laid by these animals; most of the embryos will survive nearly to the end of the incubation period and the great majority of them will show marked abnormalities (Moxon). These abnormalities concern primarily the head (hypognathia, micro- or anophthalmia, otocephaly) and the extremities (absence or deformity of individual bones, of whole extremities, etc.). Generally, head and extremities are deformed simultaneously. We have made similar experiments and can confirm these results. In addition, we find that, on the average, heterozygous Creeper embryos respond to the selenium diet of their mothers with more drastic malformations than do non-Creepers.

From our observations on Creeper and Cornish fowl it must be concluded that growth rates and gradients of developmental activity of normal morphogenesis play an important role in determining the expression of hereditary traits. This seems to apply equally to extrinsic agencies in so far as they interfere with normal development. There are many facts from vertebrate material which fit into this interpretation. Only a few can be mentioned here. A general relationship between growth rate and sensitivity to X-rays has been known since the early work of Bergonié and Triboudeau (Needham). The sensitivity of *Fundulus* embryos to X-rays parallels, in early development, the changes in mitotic index (Solberg). In Amphibia, various types of deformities can be produced by retardation of early development (Dawson); in limb transplantation experiments it was found that the more rapid is growth of the limb in the species used, the higher is the percentage of reduplication (Blount); the degree of success in inducing extremities was observed to be related to mitotic activity of the surrounding tissue (Balinsky). In chick embryos a correlation exists between the degree of susceptibility to various poisons and the regions of highest growth activity (Hyman, Buchanan, Rulon). The appearance of the hereditary flexed-tail condition of mice is preceded by a general growth retardation (Kamenoff). Similar processes seem to be involved in the embryonic origin of the polydactylous guinea-pig monster (Scott), and possibly also in otocephaly of guinea-pigs (Wright and Wagner). Morphological variations of the human vertebral column apparently are related to peculiarities of growth gradients (Kühne, Backman). Cells with high intrinsic growth potencies differ from others in their response to various physiological factors (Wertheimer). Differential growth rates, heterogeneity in metabolic activity, and the existence of "partition coefficients" do, of course, not only enter into the determination of morphological abnormalities, but unquestionably are important regulators of normal development. This is indicated by all studies concerning relative growth (Huxley, S. Wright, Green and Fekete, Lerner, and many others), and also by such observations as those on the effect of growth rates on the expression of feather patterns (Juhn, Faulkner and Gustavson; Lillie and Juhn), on eye pigmentation in *Gammarus* (Ford and Huxley), and so on.

All these facts indicate that the pattern of growth rates, as determined by the residual heredity and its interaction with the cytoplasm, influences both the expression of specific mutations and that of modifications of extrinsic origin. They account for such facts as those met with in the extremities of Creeper and Cornish embryos, and also, no doubt, for many teratological correlations, such as the simultaneous abnormalities of eyes and extremities produced genetically by the Creeper and Cornish lethal mutation, and extrinsically, by the presence of selenium in the diet. Teratological correlations of a similar type are of wide distribution among birds as well as mammals; examples from human pathology are akrocephalosyndactyly (Valentin) and the association of arachnodactyly with eye abnormalities. Even in post-natal development such syndromes can still be produced, as has been shown in experiments with baby rats, the body growth of which was suppressed by dietary protein deficiency; on recovery by refeeding, the eyes and the appendicular skeleton were the only body parts which remained abnormal (Jackson).

Differences in developmental rate also probably play an important role in bringing about many asymmetries. A case in point is the prevalence of deviation of the upper beak toward the right rather than the left side in two genetically different forms of crossbeak in fowl; this trait has been shown to trace back to size asymmetries of bones of the skull (Landauer,

1938). In our selenium experiments, we have observed that the extremities are frequently deformed asymmetrically, and that malformations of the extremities tend to be more frequent or more extreme in the left wing and right leg as compared with right wing and left leg. It is likely that these peculiarities have their origin in the lateral asymmetries of mitotic activity (Olsen and Byerly) and of developmental capacity (Rawles) which have been observed in early chicken embryos. Similar lateral or regional inequalities of embryonic growth rates may account for many of the teratological asymmetries which have been recorded for hereditary as well as non-genetic abnormalities.[1]

Beginning with Dareste many investigators have been impressed by the importance of general growth retardations for the etiology of many types of deformities. It was observed early that hybridization of distantly related forms led to the origin of complex abnormalities (Newman), and this has been confirmed more recently by Hamburger, Montalenti, and others. In his genus crosses of teleost fish, Newman observed the existence of correlations between the developmental rate in early stages and the extent of abnormal morphogenesis in later stages. But it was Stockard especially who, on the basis of experiments with *Fundulus*, postulated that complete inhibition of early development causes subsequently differential effects, the aberrations from the normal course of events being the greater the higher was the developmental rate of a particular part at the time of inhibition. This hypothesis has since been widely used in interpreting the origin of many types of abnormalities and of peculiar teratological correlations of mutational or extrinsic origin.

It is not necessary to assume, as Stockard did, that a complete inhibition of development must take place to produce abnormalities. In fact, there is definite evidence against such a conclusion. But it can hardly be denied that a great variety of genetic or non-genetic agencies, by acting on the embryo as a whole, produce specific abnormalities in localized areas. This is well illustrated in our chicken material. Though it has been shown by the beautiful experiments of Wolff that the majority of known abnormalities of chicken embryos can be produced experimentally by X-ray treatment of specific regions, the fact remains that complex and multiple abnormalities are the rule among naturally occurring teratological variations. In the instance of correlative abnormalities of head and extremities, we know that the Creeper mutation affects embryo growth as a whole before it interferes with the formation of parts. In the Cornish mutation, on the other hand, the abnormalities of head and extremities are not preceded by a growth retardation of the entire embryo. This does not militate, however, against the conclusion that a physiological process has been changed which is common to the whole embryo. In the case of selenium terata there is evidence suggesting that the effects are produced by interference with enzymes necessary in tissue respiration (C. I. Wright).

Many facts have been brought to light, especially for invertebrates, indicating the existence in embryonic life of critical and sensitive periods during which abnormalities of certain organs and parts can be readily determined. While our knowledge is scantier for vertebrates, there is little doubt that among them such periods also exist (Lehman, Balinsky, Job, Leibold and Fitzmaurice; and others).

From such observations it must not be concluded, however, that the parts specifically affected during sensitive periods are the only ones on which the particular agencies have acted. There is considerable evidence that the various "unspecific" growth-retarding factors act on the embryo as a whole, and that the localized effects are due merely to quantitative differences in physiological needs of certain parts at definite periods; these differences depending on such factors as differential growth activity, involving differential needs for certain enzymes and other substances. We do not believe that it is tenable to assume with Stockard that the abnormalities produced in certain parts and organs by general growth retardations are simultaneously impressed on the embryo and its parts at one specific period, or that they are *secondary* to effects on the embryo as a whole; nor do we think with Newman (1923) that the effect of retardation on the embryo is "more or less completely to disorganize its integrational relations". It seems much more likely from available data that the embryo as a whole is involved, there being selective responses according to specific needs imposed by varying developmental activities. In so far as it has been shown that growth activity of a particular part *within* the embryo persists after isolation (Parker), it may be concluded that the organism as a whole plays an integrational role in determining the fate of parts. In other words, with regard to the appearance of differences in growth rate the embryonic organism unquestionably has field qualities (Weiss, Huxley). With Goldschmidt, it may be assumed that varying rates of gene activity, through co-ordinated reaction velocities, set the stage for a complex pattern of developmental processes. On this stage general agents may appear, of an intrinsic or extrinsic nature, which by interfering with or by modifying certain processes in the embryo as a whole, e.g. by limiting the availability of a certain enzyme, may produce selective effects in certain parts which are to a greater extent than the rest of the body

[1] A summary of the more important human cases has been given recently (Landauer, 1939*a*).

dependent on these processes for their growth and differentiation. According to the threshold for the particular agency, such processes may cause more or less drastic deviations from normal development on one or several parts of the body, while the remainder of the embryo may show but slight changes or none at all (origin of new "constitutional types"); or, by bringing about more drastic dislocations of normal morphogenetic correlations or of normal physiological processes, they may be lethal.

To sum up, we believe that for an understanding of the developmental origin of the teratological correlations observed in our chicken embryo material it is necessary to assume that general factors are at work which act on the embryo *in toto*. The embryo and certain of its parts reflect differentially the importance which this disturbance has for their formation. Intensity of growth activity appears to be the most frequent single agency in bringing about differential effects.

In appealing to "general" factors for explanation, it must not be assumed, of course, that our problems are solved. The series of causal events always is a progression *ad infinitum*. In retracing this infinite progression we try to go from specific to unspecific, from special to general and to special again. As far as our Creeper and Cornish material is concerned, the next question relates to the specific nature of the changes which presumably produce the general effect on embryonic development.

A good deal of evidence has come to light in recent years pointing to the conclusion that a high proportion of mutations produce their specific effects by general changes in the developmental pattern of the whole embryo. Such changes may result in phenotypic variations of single organs or they may be responsible for correlative abnormalities. The physiological mechanism by which such mutations impress their effect upon the developing organism may be visualized as a resultant of changes in general processes and of varying degrees of responses in different parts of the embryo.

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LANDAUER, W. ***The Role of Unspecific Growth Retardation in the Expression of Inherited Traits (Creeper Fowl, etc.)***

The substance of this report is to be found in the following two publications, now in press:

"Studies on the Creeper fowl. XII. Size of body, organs and long bones of late homozygous Creeper embryos." *Bull. Storrs Agric. Exp. Sta.* no. 232 (1939).

"Studies on the lethal mutation in Cornish fowl. Growth in length of long bones and increase in weight of some organs." *Bull. Storrs Agric. Exp. Sta.* no. 233 (1939).

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LARAMBERGUE, M. DE. ***Races aphalliques et euphalliques de* Bulinus contortus; *recherches sur le déterminisme génotypique de l'aphallie***

Bulinus (*Isidora*) *contortus* Mich. (Gastropoda, Pulmonata), dont il existe deux variétés mendéliennes différant par la pigmentation, présente en outre un dimorphisme génital plus net. Il existe une forme **A**, euphallique, et une forme **B**, aphallique, totalement dépourvue d'appareil copulateur. Ces deux formes peuvent se reproduire par autofécondation. Dans les populations naturelles, les individus **A** et **B** coexistent en proportions variables suivant les localités.

Des élevages pédigrés, maintenus dans une stricte endogamie, ont permis de isoler et de conserver des lignées dont tous les représentants, autofécondés ou croisés *inter se*, produisent, de génération en génération, une descendance de composition sensiblement

constante. La fréquence de l'aphallie a la valeur d'un caractère racial.

On distingue en particulier les races α (plus de 95 % de A) et β (plus de 95 % de B). Quelques B apparaissent toujours dans les races α, et quelques A dans les races β, mais la descendance de ces individus sporadiques conserve la composition caractéristique de la lignée à laquelle ils appartiennent.

Quelque soit le sens du croisement $\alpha \times \beta$, une partie des hybrides F_1 réalise le phénotype A, une autre partie le phénotype B; mais les uns comme les autres produisent une descendance F_2 de composition intermédiaire entre celles des races parentes. L'élevage de la F_3 permet de reconnaître que certains individus F_2 (en majorité A) produisent une descendance α, que d'autres (en majorité B) produisent une descendance β, comme les parents, alors que d'autres (A ou B) ont une descendance intermédiaire comme les hybrides F_1. Il y a donc ségrégation.

L'hérédité de l'aphallie paraît caractérisée par une certaine labilité d'expression phénotypique alternative. Il n'y a pas d'intermédiaire entre les deux types phalliques. Cette labilité correspond peut-être à une étape évolutive vers la disparition de l'appareil copulateur et l'extension de la faculté d'autofécondation.

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LAUPRECHT, E. *Über die Vererbung des Eigewichtes bei Hühnern*

Die Ergründung des Erbganges der Leistungsmerkmale unserer landwirtschaftlichen Nutztiere gehört zu den reizvollsten Aufgaben, welche uns die genetische Arbeit stellen kann. Sehr gross sind die Schwierigkeiten derartiger Untersuchungen, insbesondere auch wegen der starken Schwankungsbreite der Leistungen sowie wegen ihrer hohen Beeinflussbarkeit durch nicht erbliche äussere und innere Wirkungen, wie z.B. Umwelt, Ernährung, Wachstum und Altern. Dazu kommen noch die bekannten Grenzen, welche der Haltung von Haustieren für Versuchszwecke gesetzt sind.

Bei Untersuchungen über bestimmte Leistungen, in unserem Falle der Eiproduktion, die über einen längeren Zeitraum z.B. ein Jahr regelmässig erzeugt werden, ist es nicht möglich, alle Versuchsbedingungen während der ganzen Dauer gleich zu halten. Wenigstens gilt dies dann, wenn die Verhältnisse denjenigen der landwirtschaftlichen Praxis entsprechen sollen.

In einem Kreuzungsversuch zwischen weissen Leghorns und weissen Wyandottes, welcher auf dem Versuchsgut Friedland der Universität Göttingen durchgeführt wurde, wurde das Verhalten der Eigewichte geprüft. Dabei stellten wir neben der F_1-Generation auch die Rückkreuzungen zu den beiden Ausgangsrassen her. Von etwa 120 Kreuzungstieren standen Legeleistungen für die Auswertung zur Verfügung. Die zunächst vorgenommene Bearbeitung der Beziehungen zwischen Eianzahl und Eigewicht ergab, dass unter bestimmten Voraussetzungen eine selbständige Untersuchung des mittleren Eigewichtes zulässig ist.

Unsere Untersuchungen sprechen für intermediären Erbgang des Eigewichtes. Die von mehreren Forschern angenommene unvollkommene Dominanz des geringeren Eigewichtes über das höhere bestätigte sich nicht. Aus den bisherigen Versuchen scheint aber hervorzugehen, dass mit einer befriedigenden mendelistischen Faktorendeutung der Vererbung des Eigewichtes innerhalb der Nutzgeflügelrassen nicht zu rechnen ist. Dagegen ist die Individualanalyse wie bei allen Nutztierleistungen überhaupt auch in der Geflügelhaltung derjenige Weg, auf welchem auf die Dauer züchterische Fortschritte erzielbar sind, selbst wenn wir im Augenblick gezwungen sind, auf eine streng mendelistische Beweisführung zu verzichten.

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LAWRENCE, W.J.C. *The Chemistry and Genetics of the Flower-colour Pigments in the Genus* Streptocarpus

The genus *Streptocarpus* is a useful source of information concerning the inheritance of chemical differences in the anthocyanin and anthoxanthin pigments. Genes have been identified controlling the production of anthocyanins, their state of oxidation and the glycosidal type; and in addition data have been obtained bearing on methylation.

Two gene pairs determine the state of oxidation of the anthocyanidin molecule. The oxidation process leading to the formation of delphinidin derivatives is usually, but not always, completed. Similarly the reduction necessary for the production of pelargonidin anthocyanins is sometimes incomplete. In species hybrids between *S. Rexii* and *S. Dunnii* conditions are less favourable for the oxidation reaction whose velocity is apparently lowered, consequently mixtures are more frequent than in the inbred garden race. The glycosidal type is controlled by a number of genes, one of which is completely dominant and epistatic. The degree of methylation has been found to depend on the state of oxidation of the anthocyanidin, delphinidin derivatives being more easily methylated

than the corresponding cyanidin derivatives. A correlation has also been established between methylation and glycoside formation, but it is not yet possible to decide which of these two processes takes place first.

Anthoxanthins are present in all flowers, and there is a pair of genes which modifies the structure of the anthoxanthin so that in one case it is a co-pigment and in the other case it is not. The co-pigment appears to have a higher competitive value than the uncopigmenting anthoxanthin.

In addition to the anthocyanins and anthoxanthins, the inheritance of a naphthquinone colouring matter, present in only two species, is being studied.

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LEMSER, H. ***Hypophysentumor und Zwillingsdiagnose***

Es wird grundsätzlich auf die Methodik der Eiigkeitsdiagnose bei Zwillingen eingegangen, insbesondere auf die Möglichkeit und die Ursachen von Fehldiagnosen. Unter anderem wird die Schwierigkeit der Eiigkeitsdiagnose an einem erbgleichen weiblichen Zwillingspaar demonstriert, von dem der eine Zwilling an einem Hypophysentumor mit ausgeprägter Akromegalie und einem Diabetes leidet, während der andere Zwilling des jetzt 24-jährigen Paares gesund ist. Die akromegale Störung entwickelte sich bei dem einen Paarling seit etwa 10 Jahren in langsam zunehmender Weise. Der Fall bietet durch den Vergleich des gesunden und kranken Zwillings die seltene Möglichkeit alle durch den Hypophysentumor verursachten somatischen und psychischen Veränderungen bis in alle Einzelheiten zu erfassen, insbesondere lässt sich die Wirkung der Hypophyse auf die Art und das Ausmass der Wachstumssteuerung im Organismus ungewöhnlich instruktiv erkennen. Ferner wird die Entstehung des Hypophysentumors bei dem kranken Zwilling und die Frage der Aetiologie der Akromegalie im allgemeinen durch das Auftreten somatischer Mutationen erörtert.

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LENZ, F. ***Was bedeutet "Erblich" und "Nicht-erblich" beim Menschen?***

Verhältnismässig einfach liegt die Sache bei gewissen Erbkrankheiten. Für die Entstehung der erblichen Taubstummheit ist ein Paar von Genen entscheidend. In diesem Fall ist das Wort "erblich" eindeutig. Eine Taubstummheit, die infolge von Scharlach entstanden ist, nennen wir "nicht-erblich". Zwar mag auch dabei vielleicht eine erbliche Disposition mitspielen; doch hat auch hier das Wort "nicht-erblich" einen bestimmten Sinn.

Unter den sogenannten normalen Eigenschaften gibt es nur ganz wenige, bei denen der Erblichkeitsbegriff so eindeutig ist, z.B. die Blutgruppen und die Augenfarbe. Bei den meisten ist die Erblichkeit viel weniger klar zu fassen. Das kann einerseits daran liegen, dass sie mehr oder weniger modifizierbar, d.h. von Umwelteinflüssen abhängig und insoweit nicht erblich sind. Es kann aber andererseits auch daher kommen, dass die meisten normalen Eigenschaften, soweit sie erbbedingt sind, nicht monomer sondern hochgradig polymer sind. Von grösster praktischer Bedeutung ist die Frage der Erblichkeit der geistigen Begabung und des Charakters. Es ist aber hoffnungslos, die Erblichkeit dieser Dinge so aufklären zu können wie etwa die des Albinismus oder die der Blutgruppen. Man begnügt sich daher meist damit, den *Grad* der Erblichkeit solcher Eigenschaften zu untersuchen. Man spricht von starker oder schwacher Erblichkeit oder auch von grosser oder geringer "Erbkraft".

Man denkt dabei wohl meist an den Grad der Ähnlichkeit von Eltern und Kindern. Dieser ist durch die Korrelationsrechnung zu erfassen. In der Tat hat man den Korrelationskoeffizienten als Mass der Erblichkeit angesehen. Er ist aber kein eindeutiges Mass der Erblichkeit. Für den Albinismus, der zweifellos völlig erbbedingt und von der Umwelt praktisch unabhängig ist, ergibt sich eine recht geringe Korrelation zwischen Eltern und Kindern, weil wegen der Rezessivität des Albinismus albinotische Individuen meist von normal pigmentierten Eltern abstammen. Und doch wäre es offenbar falsch, von einer geringen "Erblichkeit" des Albinismus zu sprechen.

Andererseits kann eine Korrelation zwischen Eltern und Kindern für Eigenschaften bestehen, die überhaupt nicht erblich sind. So zeigt der endemische Kropf eine ziemlich hohe Korrelation zwischen Eltern und Kindern, und man hat demgemäss bis vor wenigen Jahren geglaubt, dass es mit von der Erbanlage abhänge, ob jemand in einer Kropfgegend einen Kropf bekomme oder nicht. Diese Ansicht ist aber durch umfassende Zwillingsuntersuchungen Eugsters hinfällig geworden. Eugster hat bekanntlich gezeigt, dass in einer Kropfgegend zweieiige Zwillinge sich in dieser Hinsicht ebenso konkordant verhalten wie eineiige. Daraus folgt, dass die Erbmasse für die Entstehung des endemischen Kropfes praktisch ohne Bedeutung ist. Die Korrelation zwischen Eltern und Kindern hatte hier nur scheinbar Erblichkeit angezeigt. In Wahrheit ist diese Korrelation durch Umwelteinflüsse bedingt, denen sowohl die Eltern als auch die Kinder ausgesetzt sind. Der endemische Kropf ist also nicht-erblich.

Das Urteil "erblich" hängt wesentlich von der Methode ab, die man zur Erfassung der Erblichkeit anwendet. Die feinste Methode, menschliche Eigenschaften als erblich oder nicht-erblich zu erkennen, ist bekanntlich die Zwillingsmethode. Wenn eineiige Zwillinge bezüglich einer Eigenschaft im Durchschnitt stärker konkordant als zweieiige sind, oder methodologisch zweckmässiger ausgedrückt, wenn die durchschnittliche Diskordanz zweieiiger Zwillinge grösser als die eineiiger ist, so ist die betreffende Eigenschaft mindestens zum Teil erbbedingt. Auf diese Weise haben v. Verschuer und Diehl den jahrzehntelangen Streit um die Erblichkeit oder Nicht-erblichkeit der Tuberkulose im Sinne der Erblichkeit entschieden.

Die Erkenntnis, dass an der Entstehung einer Eigenschaft die Erbmasse irgendwie beteiligt ist, ist gewiss wertvoll, aber doch nicht ganz befriedigend. Man möchte gern wissen, welchen relativen Anteil die Erbmasse und welchen die Umwelt am Zustandekommen einer Eigenschaft hat. Schon Francis Galton hat mit intuitivem Scharfblick diese Frage gestellt und sie durch Erhebungen an Zwillingen zu beantworten gesucht. Seitdem hat man die Zwillingsmethode auf zahlreiche normale körperliche und geistige Eigenschaften angewandt und regelmässig gefunden, dass die zweieiigen Zwillinge stärker diskordant sind als die eineiigen. Das ist auf die Dauer langweilig. Gerade bezüglich solcher Eigenschaften besteht daher ein Bedürfnis, die Bedeutung der Erblichkeit quantitativ zu erfassen, und man hat den Anteil der Erbmasse aus dem Verhältnis der Diskordanzen zu bestimmen gesucht. Hier zeigt sich nun, dass es sehr darauf ankommt, was man unter "erblich" und "nicht-erblich" versteht.

Stellen Sie sich bitte eine isogene Population vor, das heisst eine solche, in der alle Individuen dieselbe Erbmasse haben. In einer solchen Population gibt es natürlich keine Mendelschen Spaltungen. Auch alle Geschwister sind dort erbgleich und damit auch alle zweieiigen Zwillinge. In einer solchen Population würde die Diskordanz zweieiiger Zwillinge z.B. bezüglich Tuberkulose nicht grösser sein als die eineiiger Zwillinge. Es würde also scheinen, dass die erbliche Veranlagung für die Entstehung der Tuberkulose bedeutungslos sei, und in der Tat würden die Unterschiede der Individuen dieser Population bezüglich der Tuberkulose rein umweltbedingt sein, das heisst nur von Ansteckung, Staubschäden, Unterernährung und ähnlichen Einflüssen abhängig sein. Das ist auch der Grund, weshalb die Bakteriologen an ihren Versuchstieren keine Erblichkeit der Tuberkulosedisposition gefunden haben; ihre Meerschweinchenpopulationen waren weitgehend homogen.

Die Bedeutung des Wortes "erblich", die die Zwillingsmethode voraussetzt, bezieht sich also nur auf die Unterschiede innerhalb der Population, aus der die Zwillinge stammen. Erblich in diesem Sinne heisst: In der Population kommen Unterschiede von Allelen vor, die für das Zustandekommen der betrachteten Eigenschaft von Bedeutung sind. Die Zwillingsmethode sagt im Grunde also nur etwas aus über die Homogenie bzw. Heterogenie einer Population. Unterschiede zwischen verschiedenen Populationen werden durch sie nicht erfasst; und doch machen Unterschiede verschiedener Populationen einen grossen Teil der praktisch wichtigen Erbunterschiede aus. So besteht das, was man Rassenunterschiede nennt, beim Menschen zum grössten Teil in Unterschieden verschiedener Populationen. Die so bedeutsamen Rassenunterschiede erfasst die Zwillingsmethode für gewöhnlich nicht oder doch nur im Falle rassisch gemischter Populationen. In einer gemischten Population ergibt die Zwillingsmethode scheinbar eine viel stärkere Erblichkeit von Rassenmerkmalen, zum Beispiel der Hautfarbe, als in einer reinrassigen Population; und doch sind Rasseneigenschaften in einer reinrassigen Population natürlich ebenso erblich wie in einer gemischten.

Das Zwillingsmaterial, das einer Untersuchung zugrunde liegt, entspricht in seiner genischen Zusammensetzung oft nicht der Population, aus der es genommen ist. Wenn man zum Beispiel Zwillingspaare aus der Volksschule auf Rechenfähigkeit prüft, so erhält man ein bestimmtes Diskordanzverhältnis zwischen zweieiigen und eineiigen Zwillingen. Auf diese Weise werden nur Erbunterschiede innerhalb der als normal angesehenen Rechenfähigkeit erfasst. Die Unterschiede gegenüber der mangelnden Rechenfähigkeit schwachsinniger Kinder dagegen fallen unter den Tisch, da die schwachsinnigen (debilen) Kinder in Sonderschulen zusammengefasst sind. Würde man diese mit in das Material hineinnehmen, so würde man eine stärkere Erblichkeit der Rechenfähigkeit erhalten. Entsprechendes gilt, wenn man die Erbbedingtheit akademischer Zeugnisse mittels der Zwillingsmethode zu erfassen sucht. Die Akademiker sind eben eine durch soziale Auslese relativ homogen gewordene Gruppe. Bei Testuntersuchungen hat auch die Wahl der Tests Einfluss auf das Ergebnis. In einer begabten Gruppe ergeben leichte Tests nur geringe Unterschiede und damit scheinbar geringe Erbbedingtheit der Begabung. Schwere Tests dagegen ergeben grössere Unterschiede und scheinbar stärkere Erbbedingtheit. Das gilt übrigens nicht nur für die Zwillingsmethode. In den Untersuchungen Termans über die Genetik der Begabung trat die Erbbedingtheit deshalb so stark hervor, weil er den Begriff "hochbegabt" so eng fasste, dass nur eines von 200 kalifornischen Schulkindern im Durchschnitt den Anforderungen genügte.

Das Diskordanzverhältnis von Zwillingen hängt also von dem Grad der Heterogenie einer Population ab, aber nicht nur von diesem. Ausser der Hetero*genie* ist auch die Hetero*gamie* von Einfluss darauf. Stellen Sie sich eine Population vor, in der Weisse und Neger nebeneinander leben ohne sich zu vermischen. Es würden also weisse Männer nur weisse Frauen heiraten, Neger nur Negerinnen. Mit anderen Worten, es würde in dieser Bevölkerung Homogamie herrschen. Unter diesen Voraussetzungen würden zweieiige Zwillinge bezüglich der Hautfarbe nur wenig diskordanter als eineiige sein, und die Zwillingsmethode würde zu ergeben scheinen, dass die Hautfarbe nur ganz schwach erblich sei. Daraus folgt, dass der Zwillingsforscher bei der Interpretation seiner Ergebnisse nicht einfach Panmixie, das heisst wahllose Paarung, voraussetzen darf. In unseren wirklichen Populationen herrscht weder völlige Heterogamie noch völlige Homogamie sondern eine relative Homogamie, das heisst selektive Paarung oder "assortative mating". Die Zwillingsmethode ergibt *ceteris paribus* ein umso grösseres Diskordanzverhältnis und damit scheinbar eine umso stärkere Erblichkeit je grösser die Heterogamie in einer Bevölkerung, je wahlloser also die Paarung ist.

Genau umgekehrt die Korrelationsrechnung. Die Korrelation zwischen Eltern und Kindern ist umso grösser, je grösser die Homogamie in einer Bevölkerung ist. Dasselbe gilt übrigens auch von der Korrelation verschiedener Rassenmerkmale am gleichen Individuum. Manche Anthropologen glauben noch heute, mit Hilfe der Korrelationsrechnung bestimmen zu können, welche Rassenelemente in eine Bevölkerung eingegangen sind, d.h. zu erkennen, welche Rasseneigenschaften ursprünglich zusammen gehörten. Da indessen in einer durchgemischten Bevölkerung die Gene der verschiedenen Rassenelemente sich unabhängig kombinieren, ist eine Bestimmung der ursprünglichen Rassentypen auf dem Wege der Korrelationsrechnung nicht möglich. Etwas anderes ist es, wenn ganze Erdteile oder sogar die Erdbevölkerung im ganzen betrachtet wird. Da in den verschiedenen Populationen eine relativ grosse Homogamie die Regel ist, stehen die Rassenmerkmale, wenn man die verschiedenen Populationen vergleicht, in ziemlich hoher Korrelation. Erbunterschiede der Populationen sind daher im wesentlichen Rassenunterschiede.

Eine besondere Schwierigkeit besteht bezüglich der Erfassung geistiger Rassenunterschiede. Da verschiedene Populationen in der Regel auch in verschiedener Umwelt leben, insbesondere auch in verschiedener geistiger Umwelt, könnte eine Korrelation zwischen körperlichen und geistigen Eigenschaften einer Population allenfalls auch durch gemeinsame Umwelteinflüsse erklärt werden. Die Korrelationsforschung allein genügt hier also nicht, da, wie schon oben erwähnt wurde, Korrelationen auch durch Umwelteinflüsse entstehen können. Die Rassenpsychologie stützt sich vielmehr hauptsächlich auf historische Tatsachen.

Wie wir gesehen haben, setzt die Korrelationsrechnung eine andere Bedeutung des Wortes "erblich" voraus als die Zwillingsforschung. Der von der Zwillingsforschung erfasste Erbanteil bezieht sich immer nur auf eine Population von bestimmter Heterogenie und bestimmter Heterogamie. Ausserdem sind auch die tatsächlichen Unterschiede der Umwelt, unter denen die Individuen der Population leben, von Bedeutung. Wenn wir eine Eigenschaft stark erblich nennen, so meinen wir gewöhnlich, dass sie wenig modifizierbar sei. Nun sind aber die tatsächlichen Modifikationen, welche die Zwillingsmethode in der Diskordanz eineiiger Zwillinge erfasst, nicht nur von der Modifizierbarkeit, sondern auch von den Unterschieden der Umwelt, die innerhalb der Familien vorkommen, abhängig. Wenn die Familienmitglieder unter weitgehend gleichen Umweltbedingungen leben, so ergibt die Zwillingsmethode auch bezüglich modifizierbarer Eigenschaften scheinbar geringen Umwelteinfluss oder, was dasselbe ist, starke Erblichkeit. Die Korrelationsrechnung ergibt in diesem Fall ein gleichsinniges Resultat wie die Zwillingsmethode. Wenn es keine wesentlichen Umweltunterschiede innerhalb der Familien gibt, so ist das Ergebnis beider Methoden also dasselbe, als wenn es überhaupt keine wesentlichen Umweltunterschiede in der Population gäbe.

Man darf von der Zwillingsforschung nicht voraussetzen, dass zwei Zwillinge im Durchschnitt in ebenso verschiedener Umwelt leben als andere Mitglieder der Population. Dies wirkt im Ergebnis in der Richtung eines zu grossen Erbanteils bezogen auf die Population. Da andererseits die Erbunterschiede der Populationen nicht erfasst werden, ist es nicht möglich, bestimmte Zahlen für den Anteil von Erbmasse und Umwelt am Zustandekommen normaler Eigenschaften anzugeben.

Über die Erblichkeit von Eigenschaften, die allen Menschen gemeinsam sind, sagt weder die Zwillingsmethode noch die Korrelationsmethode etwas aus. Und doch tut man gut, sich klar zu machen, dass das, was den Menschen zum Menschen macht, seine Erbmasse ist. Was den Menschen vom Schimpansen unterscheidet, ist nicht in erster Linie seine Erziehung sondern seine Erbmasse. Was ihn von der *Drosophila* unterscheidet oder gar von einer Amöbe, ist praktisch nur seine Erbmasse. Wenn also jemand finden würde, die Erblichkeit allgemeiner menschlicher Eigenschaften betrage 0·5, so wäre das offensichtlich Unsinn. Tatsächlich beträgt sie 0·999.... Im Vergleich zu dem Grundstock des menschlichen

Wesens sind die Modifikationen und damit die Umwelteinflüsse von untergeordneter Bedeutung. Insofern sind die lebenswichtigen zentralen Eigenschaften des Menschen viel stärker erbbedingt als weniger lebenswichtige periphere. Dass auch die lebenswichtigen Organe und Funktionen erbbedingt sind, zeigt das Vorkommen letaler Mutationen. Die Zwillingsmethode und ebenso die Korrelationsmethode ergibt aber gerade vorzugsweise eine Erblichkeit peripherer Eigenschaften, weil nur in diesen die Populationen heterogen sind. Die Heterogenie einer Population nimmt zu mit der Abschwächung der Auslese oder mit der Panmixie. Man kann auch sagen, je entarteter eine Bevölkerung ist, desto mehr tritt die durch Zwillingsmethode oder Korrelationsmethode erfasste Erblichkeit in die Erscheinung.

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LEVAN, A. ***The Occurrence in Nature of Asynapsis in*** **Allium amplectens**

Allium amplectens Torr. is endemic in California and Oregon. Some forms of it show almost complete asynapsis in the male sporogenesis. The asynapsis is genetically controlled and is not due to lack of chromosome homology. The asynapsis causes an abnormal course of meiosis, resulting in the formation of dyads instead of tetrads. The dyad cells are hemispherical in shape and easily recognizable from the normal crescent-shaped tetrad cells.

This condition has made it possible to study the spontaneous distribution of the asynapsis. Pollen samples have been investigated from about 150 herbarium specimens representing thirty-four counties. Asynaptic pollen turned out to be of frequent occurrence, about one-third of the studied specimens showing asynapsis. Forms with asynaptic pollen have a wide distribution in the whole area of the species, although a certain regularity in the occurrence could be noticed. Thus, sixteen of the thirty-four counties represented had exclusively normal tetrad pollen, five had exclusively dyads, while thirteen counties showed both types of pollen.

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LEWIS, D. ***The Relationship between Polyploidy and Fruiting Habit in the Cultivated Raspberry***

Cultivated varieties of raspberries can be classified into two groups according to their manner of fruiting, (1) summer fruiting and (2) autumn fruiting. The former bear their main crop of fruit on the canes formed in the previous year, in contrast with the autumn-fruiting varieties, which produce their main crop on the current season's growth. However, the autumn-fruiting varieties do form some flowers in the summer on the old canes. The summer-fruiting varieties are all diploids ($2n=14$); the autumnal varieties, with rare exceptions, are polyploids, being either triploid ($2n=21$) or tetraploid ($2n=28$). The polyploids can be distinguished morphologically from the diploids by their larger leaves and flowers, and by the white instead of grey appearance of the under-surface of the leaves, due to a more dense covering of hairs. This increased size and hairiness is undoubtedly a direct effect of an increase in the chromosome number, but the autumn-fruiting habit is not a direct expression of polyploidy. The evidence for this is that the autumn-fruiting habit is occasionally found in diploids, and that eight triploids which arose under controlled conditions by the functioning of an unreduced gamete from a diploid do not have the autumnal habit but have the other morphological characters of polyploids. Breeding experiments indicate that this habit is due to a recessive gene.

The question why the autumnal habit is rare among diploids and universal in polyploid varieties involves the relationship of polyploidy to fertility. The summer flowers of the tetraploid varieties have practically no good pollen, and consequently fertilization of these flowers must be affected by pollen of diploids. This leads to a lower fertility than when tetraploids are selfed, and also to a high proportion of triploid progeny which are inevitably of low fertility. On the other hand, the autumn flowers of tetraploids have an abundance of pollen and will be mainly pollinated by tetraploids. It is evident that there has been a rigorous natural selection favouring tetraploids which have the autumn-fruiting habit. This is an example of a gene which is probably at a slight disadvantage to the normal in the diploid, but confers a higher survival value in the tetraploid.

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L'HERITIER, P. et TESSIER, G. ***Une monstruosité physiologique héréditaire***

Nous conservons depuis six ans une souche de Drosophiles qui présente une sensibilité remarquable au gaz carbonique. Ce gaz qui, chez les Drosophiles d'autres origines, ne produit aucun effet durable, est un poison pour les larves comme pour les imagos de cette souche. Un séjour même très court dans une atmosphère suffisamment riche en CO_2 suffit à entraîner la mort. La concentration léthale minimum dépend de la température, non du gaz, Oxygène ou Azote, que l'on mélange à CO_2. Nous ne savons rien sur le mécanisme physiologique de cette intoxication.

Ce caractère physiologique est parfaitement net et se transmet dans les croisements comme un tout. Sauf dans des cas exceptionnels encore mal étudiés, on peut sans ambiguité différencier une mouche sensible d'une résistante. La souche sensible est stable. Cependant des individus résistants y apparaissent continuellement avec une fréquence faible. Ces "mutants" n'engendrent que des résistants.

Nous avons pu déterminer les règles précises de la transmission héréditaire de la sensibilité. Quoiqu' avec des modalités différentes, elle se fait par les mâles comme par les femelles. Le croisement de deux individus résistants ne fournit jamais que des résistants. Un individu sensible, au contraire, peut, suivant les cas, engendrer soit uniquement des sensibles ou des résistants, soit un mélange des deux.

Nous pensons posséder les preuves absolues que ce caractère héréditaire ne peut-être attribué ni à un système de gènes en position normale sur les chromosomes, ni à une aberration chromosomique. En effet: (1) L'utilisation de gènes marqueurs et d'inhibiteurs de "crossing-over" nous a permis de constater que les mouches sensibles transmettent la sensibilité d'une manière entièrement indépendante de leurs chromosomes. On peut en particulier, par des croisements appropriés, obtenir des individus sensibles ne possédant aucune fraction de chromosomes de la souche primitive sensible. Ces mouches transmettent la sensibilité et nous conservons depuis un an une nouvelle souche sensible ainsi établie. Il ne peut donc s'agir d'un effet retardé.

(2) Inversement on peut, par des croisements analogues, constituer des souches résistantes ayant exactement les mêmes chromosomes que la souche primitive sensible. Ces souches ne font jamais retour à la sensibilité.

(3) Le croisement simultané de femelles résistantes avec des mâles sensibles et des mâles résistants fournit, parmi les descendants de ces derniers, de très rares mouches sensibles. Ces individus aberrants transmettent la sensibilité suivant les règles habituelles. Or, dans aucun autre cas, nous n'avons observé la présence d'individus sensibles dans les descendants de couples résistants. A titre encore hypothétique, nous pensons que ce phénomène résulte de la polyspermie habituelle chez la Drosophile, la sensibilité pouvant être apportée à l'œuf par un spermatozoïde surnuméraire.

Le facteur responsable de la transmission de la sensibilité n'est donc sûrement pas de nature chromosomique et doit plutôt être recherché dans le cytoplasme des gamètes. Malgré l'échec de plusieurs tentatives de contamination par contact, nous ne sommes pas en mesure de décider s'il s'agit d'un virus ou d'un organism cellulaire.

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LINDEGREN, C.C. ***Excessive Serial Two-strand Crossing-over in*** **Neurospora crassa**

Genetical analysis of crossing-over in *Neurospora* has shown that only two of the four strands participate in most of the cross-overs. The chromosomes were divided into regions with genes as markers. When exchanges occurred in both of two such marked regions, the same two strands that exchanged in the first region usually exchanged in the second region also. Those cases in which the two strands not involved in the first exchange participated in the second exchange (four-strand exchange) were rarest. In half of the two-region exchanges, the same two strands participated; in three-tenths three-strands participated and in two-tenths, four strands participated.

Various members of the Morgan School have found that the four strands of the attached-X-chromosomes cross-over at random in multiple exchanges. But Bonnier working with the same material did not obtain the same result. *Neurospora* has many superiorities over *Drosophila* for this type of analysis, and the repeated confirmation of our finding in our laboratory suggest that the *Drosophila* results may be misleading due to the abnormality of the chromosomes, their length, and complexity (due to "repeats") as compared to the simpler, shorter, relatively "normal" *Neurospore* chromosome.

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LINDSTROM, E.W. ***Analysis of Modern Maize Breeding Principles and Methods***

The newer maize-breeding methods, comprising inbreeding plus controlled heterosis, afford an unusual case of integration of theoretical and applied genetics, particularly as they are being utilized on so vast a scale in the U.S.A. The study of such germplasm, tens of thousands of inbred lines and their hybrids, gives a good clue to the biological components of this species and their reaction to varied climatic and soil environments. With recent advances in synthesizing newer inbreds by backcross techniques and various inbreeding procedures, there is emerging a comprehensive experimental demonstration of microevolution so that evolutionary agencies of selection, hybridization, inbreeding and mutation may be properly evaluated. This, coupled with an intensive cytological study of the details of the ten maize chromosomes, is affording a clear picture of evolution in action.

There is not time to present an introductory state-

ment of the earlier developments and techniques of hybrid corn. Jenkins (1937) has recently surveyed the corn improvement programme of the U.S.A. thoroughly, giving the results and established methods used in the production of inbred lines, single crosses, three-way cross, double crosses and topcrosses.

From a genetical standpoint, a striking aspect of the maize research is the nature of the inbred lines themselves as they represent the component parts of the species. For practically 20 years now, modern corn breeding has been intensively pursued by a large group of experimenters who started sampling the germplasm of our best-bred varieties, many of which had been improved to a high level. Earlier experiences had demonstrated the plasticity of this cross-fertilizing species, and yet the practical ceiling of improvement by selection seemed to have been reached. As a matter of fact there were indications that over-zealous breeders were dragging yields slightly downwards by too close a selection to type. Ear-to-row and ear-remnant systems of half-pedigreeing seemed equally impotent at the higher levels of yielding ability.

About 1920 the inbreeding programme began in earnest, and by 1925–6 was well under way in many centres. Only one method was pursued, that of continuous self-fertilization coupled with selection within and between progenies of selfed ears. The results were uniformly similar. The selfed lines were disappointingly poor. As a matter of fact, not a single good inbred line emerged when measured phenotypically. And yet many of the lines possessed good samples of yield genes which could be combined into vigorous hybrids. The poor phenotypic character of these first inbred lines made it necessary to use them in double crosses which would overcome the low yielding ability of the inbred mother lines and permit the use of good quality seed for the commercial plantings.

Table 1. *Estimated data on maize inbred lines furnished by plant breeders*

	I	II	III
California	600	30	25
Colorado	400	50	35
Connecticut	1085	9	35
Florida	5000	50	25
Georgia	150	20	30
Illinois	5000	25	35
Indiana	100	15	30
Iowa	500	23	36
Kansas	175	25	30
Kentucky	400	15	30
Louisiana	900	50	12
Minnesota	1450	15	37
Mississippi	3500	30	25
Montana	220	60	25
Nebraska	2200	26	33
New Jersey	300	5	35
New York	1250	50	23
Ohio	260	10	37
South Dakota	700	40	16
Tennessee	187	35	—
Texas	2100	20	37
U.S.D.A.	164	18	—
West Virginia	200	6	28
Wisconsin	800	50	42
Total	27641	677	—
Average	—	28	30

Column I = total number of original selfed lines continued for 1–3 years.
Column II = number of useful inbreds saved.
Column III = average yield of inbreds in percentage of their hybrids.

The actual proportion of useful inbreds derived from this system, and their relatively poor yield are worth study. In Table 1 is presented the estimate of the breeders themselves. Column I shows the number of original lines, carried at least 2 or 3 years, after which the more serious elimination took place. Column II gives the number of useful lines emerging, a surprisingly low value, 2·4 %. This is really a maximum estimate in the sense that, of this small percentage, a still smaller number are actually to be classed as good lines. Column III shows the relative yield of these selected lines, the average value being 30 % that of their hybrids. In terms of the parental varieties, whence these inbreds were derived, the percentage yield would approximate 43. In Table 2 are shewn some actual yields over a 3-year period of selected inbred lines in comparison with their hybrids, backcross and F_2 yields. Here highly selected inbreds rate as 36·2 % in yield of their single crosses.

Table 2. *Summary of relative yields of inbred-hybrid combinations. Means of 3-year tests in percentage of F_1 yields*

	Combination	Relative yield
Inbreds	*A*, *B*, *C*	36·2
F_1	*AB*, *AC*, *BC*	100·0
Backcrosses	*AB.A*, *AB.B*, *AC.A*, *AC.C*, *BC.B*, *BC.C*	71·7
Three-way crosses	*AB.C*, *AC.B*, *BC.A*	102·3
F_2 generations	*AB*, *AC*, *BC*	65·8

This quantitative picture of the inbred lines is not altogether complete because it does not stress the really poor phenotypic nature of these original inbreds. Every one is seriously defective in one or more characters in addition to its poor yielding ability. Nor do the above data give a true estimate of numbers of lines tested, because they include only the older phases of the corn programme. Within the last 5 years, fully three times as many new inbreds have been isolated, so that the total may be estimated as nearly 100,000 lines which have been under test for at least 3 years. As far as our knowledge goes there

have not been any miraculous discoveries of superior lines in this material.

Genetically this is indicative of either a very large number of genes, of the blinding effects of environment in the selection programme, of a complex and intricate interaction of genes, or a failure in the method of isolating such lines. Probably all four factors are at work plus others as yet unrecognized.

There is no critical experimental evidence available on these points. Doubtless many genes are involved, but one might expect that among more than 30,000 lines, themselves the end-result of selection both natural and artificial, especially with continuous selection in *progeny* tests, that at least one or two superior lines would emerge which would approach the mean yield and vigour of the parental varieties.

It is certainly true that environmental fluctuations in maize hinder and prevent very efficient selection within progenies. Maize inbreds are unusually sensitive to climatic, soil, moisture and disease conditions. But when it is realized that huge numbers of inbred *progenies* are scrutinized yearly under many different environments, this barrier would not seem to be the limiting factor.

The experienced corn breeder is sometimes forced to the conclusion that gene interaction, largely complementary action, is at the bottom of the difficulty, and yet this is but another way of stating that numerous genes are involved. One gets the impression that a vigorous corn hybrid is like a mixture of enzymes in which the whole effect is far greater than the sum of its parts, in this case the contributions of the inbred lines. Until we understand gene action better, however, it is futile to speculate on this point.

There still remains the possibility that the poor quality and yield of the inbred lines trace to the system of inbreeding. With the very rapid fixation of genes in the homozygous condition by that most intensive system of inbreeding, self-fertilization, it is quite possible that a few, relatively poor, genes are fixed early in each inbred line, and no matter what the later pressures of selection are, these poor genes cannot be unfixed. In another approach to this viewpoint, Jenkins (1935) has shown that the characteristic good yield genes of an inbred line are already fixed by the second generation of inbreeding, and no later selection augments their number.

Empirical experience in animal inbreeding points in the same direction. Most of the earlier inbreeding experiments with poultry and other animals, using the most intensive methods of inbreeding (brother-sister and sire-daughter), have largely resulted in failure. With this in mind, we began inbreeding experiments in our laboratory with poultry, rats and mice, using milder forms of inbreeding at the beginning and only in later generations the intensive forms. Our inbred strains of poultry, rats and mice have now been inbred for more than twelve generations, and have maintained a high degree of fertility and vigour.

To test this point in maize, the following experiment was inaugurated 10 years ago. Due to losses from drought in 1934 and 1936, the experiment is only now nearing completion. In Table 3 is shown the plan of inbreeding, in which mating system number 1, at one extreme, uses the most intensive form of inbreeding in the early stages, and mating number 4 at the other extreme uses the milder form of sib mating at the beginning, followed by full self-fertilization. Methods 2 and 3 are intermediate. Ten lines were used in each system. The four systems of mating have approximately the same theoretical percentage of homozygosity, differing only in the third decimal place. Phenotypically the progenies in mating system number 4 are slightly superior in vigour and size of ear (yield tests in 1939 are being completed, and the lines are also being topcrossed on a common variety to test for their yield prepotency). All ten lines were maintained throughout the 8 years in systems 2, 3 and 4. In system 1, the best efforts could not save one line from extinction, and a second line is really too poor to carry on. However, final

Table 3. *Intensity of inbreeding experiment*

	I		II		III		IV	
Generation	System	p	System	p	System	p	System	p
0		0·500		0·500		0·500		0·500
1	*	0·375	*	0·375	*	0·375	*	0·375
2	S.	0·187	*	0·312	*	0·312	*	0·312
3	S.	0·094	S.	0·156	*	0·250	*	0·250
4	S.	0·047	S.	0·078	S.	0·125	*	0·203
5	*	0·047	S.	0·039	S.	0·062	S.	0·102
6	*	0·035	*	0·039	S.	0·031	S.	0·051
7	*	0·029	*	0·029	*	0·031	S.	0·025
8	*	0·023	*	0·024	*	0·023	*	0·025
% homozygosis		0·977		0·976		0·977		0·975

S. = selfed; * = sibbed; p = percentage heterozygosis.

results will not be available for another year, as at least two seasons' tests are necessary.

It seems reasonable to suppose that milder inbreeding at the beginning of a line not only would prevent too rapid a fixation of deleterious characters, but would also provide a broader base for selection under more diverse environmental conditions. Whether or not the results of this slower process of inbreeding can be equally well attained by merely using larger numbers in a continuous self-fertilization programme remains to be seen. Certainly where germplasm variance is limited, this problem should be seriously considered.

In our laboratory, we have purposefully set out to plan a long-time programme to synthesize the corn species from our first-cycle lines (those produced by self-fertilization from varieties) which may be considered the primary building blocks. Recalling that they have retained less than 50 % of the yield of their parental varieties, it becomes of evolutionary interest to ascertain how rapidly they can be stepped back again to their original level. We have taken only one method on which to operate, namely, the backcross method. We term the second improvement stage as the building up of second-cycle lines from the first cycles. There are other techniques, such as the continued isolation of new lines from single or double crosses of the first-cycle lines.

We have now completed the second-cycle programme on our first block of inbred lines, a programme which requires 7–8 years. Our plan has been to backcross once or twice to the recurrent parental, first-cycle inbred, followed by five to six generations of inbreeding (including sibbing and, later, selfing). We have discarded hundred of lines using three or four backcrosses because, for most lines, such an amount of backcrossing has driven the lines so far back to the original recurrent inbred that no practical residue of variability has remained for efficient selection.

A lot of forty second-cycle lines has thus been fixed. Choosing twenty of the best, we have compared their actual yields with the best ten first-cycle lines. Where selected first-cycle lines averaged in yield 43 % of the parental varieties, the second-cycle lines average 56 %. Phenotypically the second-cycle lines are noticeably superior to their progenitors, especially in general vegetative vigour, pollen production (under drought conditions), lodging resistance and disease resistance. Of course, these second-cycle lines have not the same percentage of homozygosity as the original lines, but the differences are small (less than 2 %).

Whether or not these second-cycle lines, produced and bred wholly for phenotypic characters, retained the valuable, selected yield genes of their first-cycle lines has been under test for only one year. In 1938 eight of the lines were tested in paired comparisons with their original first-cycle lines, being topcrossed on a common variety (Table 4).

Table 4. *Yield differences of first- v. second-cycle inbreds in topcrosses.* 1938 test

Inbred lines	Average yield in lb.	Difference
Idt	26·1	—
Idt (Ldg)	28·9	+2·8±0·92
Idt (Baw)	23·9	−2·2±0·92
Osf	22·1	—
Osf (KR)	25·3	+3·2±1·27
Osf (I_{66})	23·2	+1·1±1·27
Ldg	23·9	—
Ldg (PR)	24·4	+0·5±1·0
Ldg (Osf)	23·2	−0·7±1·0
TR	24·7	—
TR (Ldg)	25·5	+0·8±1·0
PR	23·5	—
PR (Osf)	21·6	−1·9±0·8

Second-cycle lines are those with parentheses which enclose the non-recurrent parental inbred. Standard errors used in difference column.

Of the eight second-cycle lines, two, Idt (Ldg) and Osf (KR), were significantly better, four were about the same and two were slightly poorer. Apparently one or two backcrosses, coupled with the usual field and ear selection, are sufficient to retain most of the valuable yield genes, originally fixed.

The third cycle was begun in 1938 by backcrossing single crosses of two second-cycle lines to the parental inbred most likely to bolster up the weaknesses present. It would not be surprising if the third-cycle lines in 1945–6 should still be below the original yield of the variety. A 10 % improvement in yield would still leave them at a figure of 66 % where the original variety was 100 and the first-cycle lines were 43. At a similar or decreasing rate it would require at least five to six cycles of improvement with this method to attain their original level, which may not be surprising in view of the genetical complexity present.

In addition to their morphological (vegetative) and yield-prepotency differences, maize inbred lines have proved to possess a high degree of physiological individuality, marked differences in root systems, and striking differences in resistance to diseases. Physiological individuality has been demonstrated in our laboratory by the use of mineral nutrient solutions. The first work done by Smith (1934) showed particularly the differential responses of inbred lines to phosphorus. More recent work by Harvey (1939) verified these results, and demonstrated similar differences in nitrogen response, especially to the nitrate v. ammonium ions. Hybrids of efficient by inefficient users of phosphorus or nitrogen invariably

resulted in a dominance (or interaction) of the efficient type.

Recent unpublished investigations have given quantitative evidence of hereditary differences in top-root ratios of the various inbred lines, whether grown in water, sand or soil cultures. Inbreds possess marked differences in types of root systems, varying significantly in the degree of fibrousness, number, size and angle of penetration of the main roots.

In the matter of disease resistance, the complexities of the parasite (smut or rust), and the troublesome environmental fluctuations of the corn-ear rot infections, have militated against a clear genetic solution of resistance, and likewise against isolation of highly resistant lines to such pathogens. In the case of bacterial wilt (*Bacterium stewarti*), however, the recent work of Wellhausen (1937*a*) has shown clearly the genetic basis for resistance as traceable to three pairs of supplementary genes, each showing dominance. Wellhausen (1937*b*) also pointed out certain basic relations in the problem of virulence which have now been fully verified and extended by Lincoln (1939) in our laboratory.

Bacterial virulence has been shown to increase by passage through, and reisolation from, highly resistant inbred lines of maize, and to decrease by passage through susceptible lines. This has been demonstrated both for ordinary bacterial cultures and for single-cell strains. Lincoln has traced the agents responsible for this host-parasite interaction, and found them to be mutation (with rates similar to those in higher plants and animals) plus differential growth of virulent or avirulent strains in the resistant or susceptible hosts.

The genetic problem of heterosis still remains unsolved. Orthodox explanations of gene interaction, usually dominance of linked genes, fit the case reasonably well, but no critical data have yet appeared. Richey and Sprague's (1931) convergent improvement tests are an attempt in this direction, but need extension. Ashby's (1930, 1932) reports on relative growth rates of inbreds and hybrids are descriptions of heterosis, but do not bear on the genetic basis of heterosis, except that the effects of hybrid vigour are usually manifest in the embryo. His statements on the inheritance of growth rates are hypothetical. East's (1936) hypothesis of multiple allelic size genes is, of course, in need of experimental testing.

We have run large series of growth curve experiments and find that, given inbreds and hybrids with approximately the same season of growth, there is no great difference in relative growth rates (measured logarithmically) between inbred and hybrid (Lindstrom, 1938). We have evidence of small differences in relative growth rates between inbred lines (or hybrids) at various stages of growth, each inbred (or hybrid) being individually slightly different in the period of growth when it attains its highest rate.

When early v. late inbreds and their reciprocal hybrids were compared for their relative growth rates, differences were manifest. Seven sets of such crosses were tested for their rate during the first 6 weeks of growth in the greenhouse where environmental control was most satisfactorily obtained. A composite picture of the results appears in Fig. 1, which

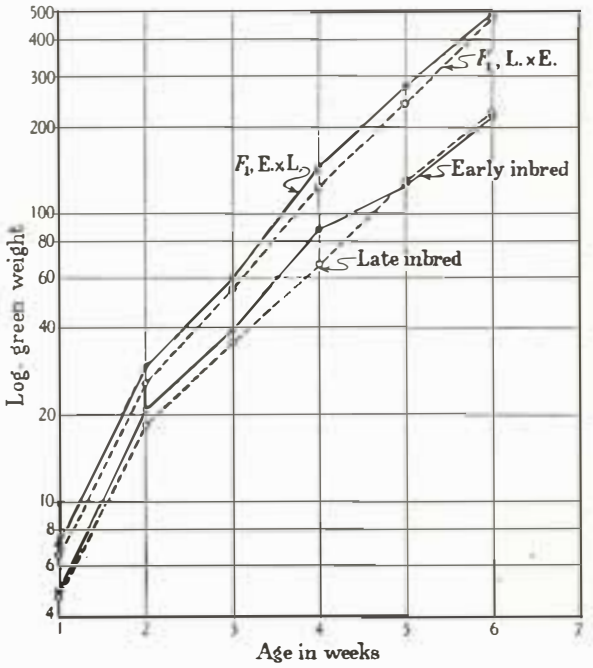

Fig. 1. Growth curves of early and late inbreds and their reciprocal hybrids.

is based on average green weights of twenty plants at each week for each strain. The log. curves show a difference in rate between inbreds and hybrids which is statistically significant when tested by analysis of variance.

The interesting point seems to be that the hybrids inherit the more rapid growth from the early inbreds in the first portion of the curves (up to 4 weeks), and thereafter they inherit the more rapid growth from their later parental inbreds. The data also show that these hybrids begin their growth with an embryo considerably larger than that of the inbreds. Heterosis begins early, and the highest rates of growth are in the early stages. The hybrid maintains its early advantage over a longer period of time than does the inbred. In these crosses a small, significant maternal effect may be noted in the reciprocal hybrids.

Future problems of the maize programme point in at least two directions. First, there must be a continuous synthesis of maize germplasm as represented in the inbred lines. At present there is a

comprehensive programme under way to combine the best qualities of inbreds from various sources in the corn belt of the U.S.A. by hybridization and subsequent selection from backcross methods or by straight inbreeding. Next the germplasm from more widely diverse localities, even from North and South America, will be integrated.

Second, there is the breeding of hybrids (double crosses, topcrosses or even single crosses) for special purposes such as for specific soil types or levels of fertility, and for specific uses as carbohydrates, oil or protein in the milling and chemical industries.

From the standpoint of genetical theory, we need to explore the actions of genes *en masse* as they interact with one another and with their environment. The genetics and biochemistry of hybrid vigour need further experimentation, particularly as they relate to gene interaction.

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LOCKHART-MUMMERY, J.P. *Somatic Mutation as a Cause of Tumours*

The only possible form of gene mutation occurring in a somatic cell which could be obvious, or of any practical importance, must consist of, or be accompanied by, an increased rate of division as compared with the normal for that cell. Should this happen then it is evident that in course of time an island or colony of such mutated cells would form among the normal cells; a tumour would in fact be produced.

The somatic mutation theory of tumours postulates that as a result of some cause, or causes, a gene mutation occurs in a somatic or autosomal cell resulting in an increased rate of division.

This theory of the causation of tumours appears to fit all the facts known about tumours at the present time.

The theory attempts to explain the actual manner by which a normal cell is converted into a tumour cell, but does not attempt to explain the causes of this change. It is not opposed to the virus theory, since the latter attempts to explain the cause for the change and not the way in which it occurs.

The difference between innocent and malignant tumours, it is suggested, depends on the growth rate of the tumour cells.

Numerous attempts have been made to substantiate this theory by experimental means, some of which have been partially successful.

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LÖRTSCHER, H. *Ursachen der Variation der Jahresdurchschnitte einer Milchviehherde*

Als Grundlage jeder Auswertung von Milchleistungserhebungen bezweckt die Eigenschaftsanalyse die Ausschaltung der durch die nichterblichen Umwelteinflüsse verursachten Variation. Die in diesem Sinn versuchte Ausscheidung der verschiedenen Variationsanteile nach ihrer Ursache bei den Kontrolljahresleistungen einer grossen British-Friesian Herde, führte unter Berücksichtigung von vier je acht Jahre auseinanderliegender Herdedurchschnitte (1912, 1920, 1928 und 1936) zu folgenden Ergebnissen.

Von der Totalvariation der absoluten Kontrolljahresleistungen entfallen 44 % auf die Variation *zwischen* den Jahren und 56 % auf den Anteil *innerhalb* der Jahr. Der Einfluss des Alters, der Dauer der Trockenzeit und der "service-period" macht rund 10 % und derjenige des Kalbemonats 5·4 % der Totalvariation aus. Die Variation zwischen den Jahren wird zu etwas mehr als einem Drittel durch die wechselnde genetische Zusammensetzung der Herde im Laufe der Jahre und nur zum Rest durch wechselnde Jahreseinflüsse verursacht. Die nach Ausscheidung der erwähnten Umwelteinflüsse übrig bleibende Variation innerhalb der Jahre nimmt im Jahre 1920 wenig, 1928 dagegen um das dreifache und 1936 um das doppelte des vorhergehenden Jahres zu. Die Zunahme im zweiten und vierten Jahr ist vornehmlich dem Einfluss günstigerer Produktionsverhältnisse, diejenige im dritten Jahr hauptsächlich

züchterischen Einflüssen zuzuschreiben. Dieser Befund wird durch die Veränderung der Inzucht- und Verwandtschaftsverhältnisse in der Herde im Laufe der vier betrachteten Jahre bestätigt. Die mittlere Inzuchthäufigkeit stieg von 0 % im Jahre 1912 auf 0·3 % im Jahre 1920 und der mittlere Verwandtschaftsgrad von 1·0 % auf 1·5 %. Diese Werte entsprechen der Anwendung von gewöhnlicher Reinzucht ("out-breeding"), welche keine wesentliche Veränderung der genetischen Variation erwarten lässt. Dagegen sprechen die 1·6 % mittlere Inzuchthäufigkeit und 8·7 % durchschnittliche Verwandtschaft im Jahre 1928 für die Anwendung von Linienzucht, welche eine Erhöhung der genetischen Variation mit fortschreitender Generationenfolge bedingt. Im Jahre 1936 beträgt der mittlere Verwandtschaftsgrad 20·9 % bei 4·9 % mittlerer Inzuchtstärke. Diese starke Erhöhung der Verwandtschaft deutet auf eine Kombination der Linien innerhalb der Herde hin und beschränkt wahrscheinlich die durch die erhöhte Inzuchthäufigkeit zu erwartende Steigerung der genetischen Variation in diesem Jahre.

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Love, R.M. ***The Role of Cytology in Wheat Improvement***

Modern Canadian wheats must combine the attributes of a number of varieties (and even of species). Special problems arise out of this necessity. Thus, wheats differing widely in their origins are being used as sources of earliness, yield and resistance to disease, drought and insects. The parent varieties used also differ markedly in their genotypic and often chromosomal constitutions. Cytological investigations are more urgent under these conditions than formerly when nearly all crosses involved varieties of *Triticum vulgare* only, and therefore would not be expected to exhibit the degree of irregularity found among derivatives of wider crosses.

The application of cytology to wheat improvement may be conveniently divided into two phases; study of hybrid material, and the origin of off-types.

(1) *Hybrid material.* (*a*) New varieties of polyploids of hybrid origin are not, as a rule, as uniform as are the older, standard varieties, either in their visible characteristics or in meiotic chromosome behaviour. In order to ascertain the degree of meiotic stability of the more promising new rust-resistant spring wheat sorts, young pollen tetrads are examined and the number of micronuclei per hundred determined. Seed from the most stable plants is used for propagation.

(*b*) Of 336 *vulgare*-like rust-resistant plants of the fifth, sixth and seventh generations of pentaploid crosses studied cytologically, no less than 15 % exhibited specific irregularities in chromosome behaviour—due to rearrangements of chromosome segments which had occurred. Further selection should result (as it has done with others, see (*c*) below) in lines homozygous for one or more of these alterations. They will not then appear as irregularities but will be the chromosomal set-up for the new varieties. When such lines are crossed with other sorts, however, the alterations will again lead to irregularities in F_1 and later generations.

(*c*) F_1 *studies.* A detailed examination of meiosis in F_1 hybrids (fifteen pentaploid and fourteen hexaploid) has shown, in most cases, specific differences in the arrangement of chromosome segments in the parents.

(2) *Off-types.* The polyploid nature of *vulgare* wheats complicates the task of the plant breeder and the producer of pedigreed seed stocks. The presence of six sets of chromosomes, some members of which appear to be partially homologous, is known to be the cause of the origin of many speltoid and compactoid forms as well as other off-types.

For many years the Canadian Seed Growers' Association has experienced great difficulty in maintaining pure-breeding strains of Dawson's Golden Chaff winter wheat. A number of off-types arise spontaneously, the most notable having white chaff. Cytogenetic studies conducted since 1935 show that most (if not all) owe their origin to losses of chromosome segments or even whole chromosomes. Furthermore, by cytological examination, plants phenotypically indistinguishable from the normal have been detected which gave rise to off-types in later generations. At the same time lines have been isolated, by means of combined cytological and morphological examination, which breed true to type. In varieties such as this, however, eternal vigilance is the price one has to pay in order to maintain a high standard of stability.

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Ludford, R.J. ***Can Somatic Cell Mutations Explain the Properties of Malignant Cells?***

The one property common to all malignant cells is their capacity for unlimited, uncontrolled proliferation. Physiologically, they are characterized by a high aerobic glycolysis—[a] property not specific for malignant cells. Cytologically, they are characterized by abnormalities of cell division. Wide variations occur in the number of chromosomes, which are frequently atypical in structure, and precocious splitting at the prophase is of common occurrence. The mitotic spindle is often abnormal, and chromosome formation sometimes occurs without the development of a spindle.

The malignant cells of different tumours exhibit wide variations in their rate of growth and degree of cellular differentiation. The cells of the various strains of transplantable tumours exhibit their own specific cytological characters. These are retained after prolonged periods of transplantation in animals, and growth in tissue cultures. The malignant cells of different strains vary in their reactions to the acid vital dyes, and in their ability to grow in a fluid medium *in vitro*. Physical and chemical agents which arrest mitosis in normal cells exercise the same action upon malignant cells. The evidence available indicates that in general malignant cells are slightly more sensitive to injury than their normal prototypes.

While there is no one definite morphological criterion of malignancy, yet the cells of the various strains of transplantable tumours present features which distinguish them from their normal prototypes. Thus in tissue cultures the nuclear membranes of malignant cells are usually more clearly defined, the mitochondria usually finer and more numerous, and the cytoplasm more granular. Whatever be the cause of malignancy, one fact is clear, viz. that malignant cells are specifically altered cells, and not merely normal cells excited to increased proliferation.

In the case of certain neoplasms—the so-called filterable tumours—a particulate agent, or virus, can be separated from the malignant cells, which is capable of transforming normal cells into malignant ones. The active agent of any one tumour produces only that one type of tumour; that is, each agent acts only on one type of cell and induces its own special cytological changes, which also are retained after prolonged periods of growth both *in vivo* and *in vitro*.

Is the malignant transformation brought about by some alteration in the genes of normal cells, or can somatic cells be constitutionally altered in some as yet unknown manner, so that specific cytological characters are transmissible independently of the gene mechanism?

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Ludwig, W. ***Bemerkungen zur Chiasmabildung und zur Interferenz***

In **V**-förmigen Chromosomen erhält man oft zwischen einem kleinen die SFA umschliessenden Intervall und einem kleinen benachbarten Intervall Koinzidenzwerte über 1. Die einfachste Erklärung hierfür ist, dass die SF-Region jedes Chromosoms oder Schenkels in einem Teil der Fälle an der zur Chiasmabildung führenden Paarung nicht teilnimmt (Kikkawa). Durch diese *Asynapsis* könnte auch der oft hohe Prozentsatz der Bivalenten ohne Chiasma erklärt werden (*X* von *Drosophila melanogaster* 4-5 %). Dass sich die Chiasmen in jedem Bivalent räumlich-zeitlich in der Richtung SFA → distal anlegen, ist zwar von vorn herein plausibel, weil verschiedene Prozesse (Terminalisation, Trennen) in dieser Richtung ablaufen, aber bisher völlig *unbewiesen*. Die zytologischen Indizien sind spärlich und nicht widerspruchsfrei. Mather's Schlüsse (1936) sind nicht beweisend. Denn führt man seine Rechnungen nicht für die Richtung SFA → distal, sondern für die umgekehrte Richtung durch, so ergibt sich ein Resultat, aus dem man mit gleichem Recht auf eine Chiasmabildung distal-proximal schliessen kann (Boost unveröff.). Heute kann nur gesagt werden: (I) es ist wahrscheinlich, dass sich die Chiasmen hintereinander anlegen, (II) ein Anlegen SFA → distal ist mit der Erfahrung im Einklang. Punkt (I) ergibt sich als Wahrscheinlichkeitsschluss aus obigen Erwartungen und aus einer früheren Methode des Verfassers (drei- und mehrfache "crossing-over"). Für Punkt (II) ergibt sich: Bei den Annahmen, dass (*a*) die SFA wie ein ständiges Chiasma wirkt, sich (*b*) die Chiasmen proximal-distal anlegen, dass es (*c*) für jedes Chromosom eine modale Chiasmadistanz gibt und (*d*) die Kurven für das erste, zweite usw. Chiasma binomialen Charakter haben, erhält man eine Gesamt-Chiasmaverteilung, welche auch in Einzelheiten mit der empirischen übereinstimmt, jedoch nur bei Annahme einer partiellen Asynapsis in der SF-Region (Boost; alle erreichbaren Versuche an *D. melanogaster* X, II, III und *D. virilis* X). Die Unterschiede der Interferenz zwischen verschiedenen Chromosomen (*virilis* X < *melanogaster* X < *melanogaster* II + III) und innerhalb jedes Chromosoms (distal > proximal) sind wahrscheinlich real und erstere wahrscheinlich bedingt durch verschiedene modale Chiasmadistanzen. Mather's Erklärung mit verschieden starker Lokalisation des ersten Chiasmas ist bei Verwendung der neuen Speicheldrüsenkordinaten kaum mehr möglich; jedoch kann Differential- und Interferenzabstand verschieden sein. Das Absinken der Interferenz gegen die SFA ist durch die Asynapsis erklärbar. Versuche mit Inversionen bestätigten das Ergebnis einzelner Autoren, dass die Häufigkeit des Nichttrennens niedriger sein kann als die Häufigkeit der Bivalenten ohne Chiasma. Also ist (auch als Regel) Chiasmabildung nicht notwendige Vorbedingung für normales Trennen.

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Lundholm, I. ***Inheritance of Hypochromic Anaemia***

With the exception of pernicious anaemia the most frequent type of anaemia nowadays is hypochromic anaemia which is more frequent in women than in

men. On material from Sweden it has been shown that it is particularly frequent in women after the age of puberty and before the climacteric. By using Dahlberg's "later siblings' method" it is shown to occur among sisters of patients with a frequency of $41 \pm 6{\cdot}6\,\%$. It is further shown that 50 % of the mothers have the disease. It cannot be recessive and appears to be dominant in women with a penetrance rather below 100 %. The following hypothesis is propounded. If somebody has the gene of the disease, the latter in most cases does not manifest itself unless there is a loss of iron through bleeding. Normally iron circulates in the body, and the daily amount needed for maintaining a normal haemoglobin standard is probably very small (a few mg. a day). After bleeding, normal persons rapidly absorb iron. Persons who have a hereditary disposition to the disease cannot rapidly resorb iron from normal food and consequently develop a hypochromic type of anaemia. Since bleeding is a normal phenomenon in women, they practically always develop the disease between, say, 15 and 50 years, if they have the gene. Men only reveal the gene if they have haemorrhoids, bleeding ulcer, and so on. In rare cases men suffer from the disease, although no bleedings can be discovered. It is possible that infections, lack of vitamins and other abnormal factors may reveal the disease in exceptional cases in men and women carrying the gene. According to the hypothesis advanced the gene causes some abnormality in the digestive tract which results in a decreased power of resorbing iron. Since loss of iron is normal in women, the disease is chiefly limited to them. By administering large doses of iron the resorption is increased and the patient recovers.

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LUSH, J.L. ***Methods of Measuring the Heritability of Individual Differences among Farm Animals***

The ideal method of estimating the degree of heritability of a characteristic is to compare the variance of that characteristic in the original population with the average variance within isogenic lines derived from that population. But in populations of farm animals the only isogenic lines available are identical twins; even those are rare and may show some likeness from common maternal environment. Next best is an experiment with selection in opposite directions continued over several generations. The difference produced in the population means, when divided by the amount of selection practised, gives an estimate of the amount of the initial variance which was additively genetic but includes a little of the epistatic variance. The most widely applicable methods of estimating heritability in farm animals are comparisons of the amount of resemblance or difference between animals variously related by descent. Such estimates include the additively genetic portion of the variance, part of the epistatic variance and, in some relationships, part of the variance caused by dominance deviations from the additive scheme. The major pitfall in interpreting such resemblances is the difficulty of appraising correctly the environmental contributions to the observed resemblances between various kinds of relatives. A minor pitfall is that the mating system may differ from random mating more or less than the observer estimates.

Where heritability is being estimated from the resemblance between relatives:

(*a*) The most dependable estimates are based upon the closest relationships, because the sampling errors are thereby kept small relatively to that which is being estimated.

(*b*) The correlation between parent and offspring is generally the most useful approach, if environmental correlations can be adequately discounted. The correlation between dam and offspring within groups of offspring all by the same sire is a very useful way of automatically discounting most environmental correlations and deviations from random mating, although it leaves differences between groups of dams unanalysed. If the parents have been highly selected the regression of offspring on parent must be used instead of the correlation.

(*c*) Full sib resemblances include something from the dominance deviations and are apt to have been affected more by common environment than are parent-offspring resemblances.

(*d*) Paternal half-sib resemblances are generally more informative than maternal half-sibs, because the latter are likely to include some resemblance from common environment in their pre-natal and pre-weaning period.

(*e*) Relatives more remote than half-sibs are rarely of much use for estimating heritability, since the genetic correlations expected are small relatively to their sampling errors.

(*f*) Regression of variance within individual pairs on the relationship of the two members of the pair to each other seems a good way to combine in one figure the evidence from all kinds of relationships in a population in which the relationships are intricate, as in a small herd long closed to outside blood. One can thus include irregular relationships not described by the common verbal terms. This regression is curvilinear because of dominance and epistasis.

(*g*) The genetic element in the differences between herd averages is difficult to appraise.

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MA, SUNG-YÜN. ***Experimental Studies on the Induction of Heat Modifications in*** **Drosophila melanogaster**

Eggs, larvae, prepupae and pupae of a long-inbred Oregon wild stock, reared at 25° C., were shocked with high temperatures, ranging from 38·5 to 41° C., in various developmental stages. Care was taken in maintaining the accuracy in timing the material (physiological ages), the exactness in heat treatment and the constancy of the developmental conditions, so that a number of modifications was induced in high percentages. The heat mortality is generally high in earlier developmental stages and lower in later ones; within each stage it is high at the very beginning and at the end (including the moulting period), but low in the middle part (except in the pupal period where another high mortality seems to exist at 30 hr. stage). It plays therefore a considerable selective role during the heat treatment, if the variation of the physiological age of the population is too great. The modifications, being specific to the developmental stages and to the intensity of shocking, may be given together with their corresponding sensitive periods below (the numerals represent the number of hours after the beginning of the stages indicated; those italicized, the optimal periods; E = embryonic period; L I, II, III = first, second, third larval instars; P = puparium formation): Wings: (1) Extracross-vein, extra-vein and cross-veinless, late LIII–P 30; (2) Swollen with lymph (long shocked), P 30; (3) Shedding of marginal hairs, P 10–*15*–20; (4) Narrow-pointed, P 10–20; (5) Truncated, P 10–*20*–25; (6) Round-tipped, P 20–*35*–45; (7) Convex, P 0–*35*–45; (8) Concave, P 35–*70*–85; (9) Roof-like (long shocked), P 10–30; (10) Spread (strong if long shocked), P 15–75; (11) Spread and uplifted, P 70–emergence. Bristles: (12) Reduced, twisted, LIII–P 30; (13) Branched, P 25–*30*–40; (14) Small, P 20–45; (15) Hooked, P 35–50; (16) Thin, long, arrow-like and knotting, P 45–55; (17) Slightly to totally decolorized, P 50–80. Aristae: (18) Hairs branched, P 30–*35*–40. Eyes: (19) Furrowed, late LIII–P 15; (20) Rough, L III–P 60. Legs: (21) Crippled, E 10–20, LIII 22–P 12. Thorax: (22) Anterior margin dented, P 30–40; (23) Stamped dorsally, P 70–emergence. Scutellum: (24) Horny outgrowths, P 10–*20*–30. Inner tissues: (25) Tumour-like black bodies, LIII.

In the truncated wing modifications, the margin remains intact. The reduction in size is caused by a reduction of the cell size, which is more strongly expressed in the distal than in the proximal part, indicating a differential susceptibility of different parts of the wing toward temperature shock.

The sensitive periods of the bristle modifications show that the bristle-forming structure, trichogenic cells or their predecessors, may be affected in such a way as to give no more bristles, or to develop minute and distorted ones. As soon as bristle formation begins the bristles react to temperature shock by changing the direction of normal growth in a definite time-space relation, i.e. the older the bristles shocked, the more distal is the point at which the change begins, until only a knot is formed at the tip. The pigmentation of the bristles is completely destroyed shortly before the visible darkening process takes place.

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MCKINNEY, H.H. ***Virus Genes***

The virus of tobacco common mosaic was first concentrated and purified through the use of biochemical methods by Vinson and his associates (1927, 1929, 1931). Stanley (1936) obtained the virus in the form of microscopic condensates which he considered to be true crystals of a globulin. Bawden *et al.* (1936), from X-ray studies, concluded that these virus condensates are liquid crystals and not true crystals, and the results of Bawden and Pirie (1937) indicate that the virus is probably a nucleoprotein.

The virus has never been successfully increased *in vitro*, but there can be no doubt as to its ability to increase on a large scale in highly susceptible tobacco (McKinney and Webb, 1926). In the highly susceptible genotypes of *Nicotiana tabacum* L. and in many other species the virus induces light-green mosaic mottling on the foliage and stunts the plants, but does not prevent seed production. Under ordinary cultural conditions mottling occurs on all leaves appearing after infection, and virus synthesis is at a high level in all of these leaves. This virus is not known to enter the embryo, and therefore the disease is not transmitted from generation to generation in tobacco.

In addition to the light-green mottling induced by this virus there are small yellow or yellowish green spots which occasionally appear on the leaves of infected plants. Virus isolated from these atypical spots induces yellow mosaic when inoculated into healthy plants (McKinney, 1926, 1929, 1935). At first it was thought that these localized spots resulted from virus contaminants from outside sources, but all experimental evidence supports the conclusion that they are the result of mutation of the common or wild type of virus (McKinney, 1935). The viruses from these spots are not all alike (Jensen, 1933). Some induce a mild yellow mosaic, whereas others induce severe yellow mosaic on some varieties of tobacco, and white mosaic on White Burley types. These mutant viruses (strains) may be differentiated

on different species and varieties of host plants with respect to their ability to invade the tissues rapidly or slowly and on a basis of local or systemic necrosis and systemic mottling.

There is another group of mutants which cannot be detected in association with common mosaic by visual means (Holmes, 1934; McKinney, 1937). Some of these induce practically no visible symptoms in tobacco. These strains are isolated by means of several dilution techniques and by random samples of very small zones of tissue from infected leaves. When purified they also throw occasional aberrant types, some of which induce yellow mosaics. Thus we find that the common light-green mosaics throw a graded series of mutants ranging from highly virulent to highly attenuated strains with reference to their ability to impair the plastid pigments, and an attenuated virus can throw virus which is more virulent than the common or wild type.

It is noteworthy that the mutants possess essentially the same lethal temperature characteristics as the wild type of virus. This temperature is 90° C. or above *in vitro* for 10 min. exposure, and it is the highest lethal temperature known within the group of viruses which infect tobacco.

Many collections of tobacco common mosaic have been obtained from different parts of the world and all were found to mutate (McKinney, 1929). Many attempts have been made to obtain the common or wild type of virus in pure form which will induce only the light-green mottling and not throw aberrants, but all of the known methods have failed. After many series dilutions, chemical treatments and physical treatments, the capacity to mutate has not been reduced. Whether or not this capacity can be increased by suitable ultra-violet or X-ray irradiations has not been determined.

Plants or groups of plants having the pure or essentially pure aberrant mosaics are rarely encountered in nature, and from the writer's observations these cases are more rare in the cooler regions than in the regions of high temperature (McKinney, 1929, 1935).

Mutants have been isolated with greatest frequency when the diseased plants or stem-tissue cultures were maintained at high temperatures (Holmes, 1934; McKinney, 1935, 1937). An experiment was carried out with eight young tobacco plants infected with the common mosaic virus. Four plants were cultured at 22·5° C. and four at 36·0° C. At both temperatures the plants produced an average of fifteen mottled leaves per plant during the test. At 22·5° C. only two detectable aberrant spots were produced on all leaves, whereas at 36·0° C. twenty-three such spots appeared, in spite of the fact that the leaf areas were greatest at the low temperature.

So far as is known all the mutants which have been isolated by the writer, and by other workers, can be maintained true to type indefinitely in suitable plant stocks, except in so far as occasional mutants arise.

Salaman (1937) obtained several weak or attenuated strains from the "*Y*" virus of potato. These were referred to as variants, but they may be mutants. Salaman reports that all these weak strains protect the tobacco plant against the more virulent "*Y*" virus. In other words, the less virulent types dominate the more virulent "*Y*" virus. In another paper Salaman (1938) reports a like situation in the potato "*X*" virus and several of its strains.

In the case of the tobacco common-mosaic virus and its mutants it appears that a different situation obtains. Domination or protection is not always by the first virus introduced, nor is it always correlated with the degree of virulence as measured by the chlorophyll disturbance. In the writer's experiments it was found that the mutants did retard the development of the wild-type virus in tobacco, but eventually the latter did displace the mutants in the upper leaves of mature plants or in the side shoots which replaced the excised mature main stalk. The results were essentially the same when any one of the mutants was established before introducing the wild-type virus or when the plants were inoculated with a compound consisting of one mutant and the wild type in approximately equal amounts.

Following another procedure, healthy young tobacco plants were inoculated first with wild-type virus, and after symptoms were established the plants were reinoculated in the youngest tip leaves and in the stem tips with virus of a mutant. Three mutants and one secondary mutant were tested. Each of these mutants as well as the wild type moved at essentially the same rate in the plant when the viruses were not compounded. In these tests the mutants had a slight effect in a few of the tip leaves, but the common or wild-type virus exerted its suppressing influence completely and almost immediately (Table 1).

When the three mutants which were derived directly from the wild type were tested against each other in pairs it was found that the symptoms of the yellow types dominated over a mild-green type as shown in Table 1. In one pair, symptom domination and virus domination required a long time; in the other pair, symptom domination required a very long time, and traces of the mild-green mutant virus were still present in the top leaves of a branch which replaced the main stalk. The two yellow mutants from the wild type show a high degree of compatibility. If either virus is capable of complete domination a very long period of time will be required to obtain the evidence.

Table 1. *Showing the dominating influence of one virus over another when tobacco plants were inoculated with two viruses. The second virus was inoculated into the apical zone of the stem after the first virus had induced symptoms*

Tobacco common-mosaic virus, three of its mutants and one secondary mutant	Combination inoculations	Dominant virus	Relative rate of domination
W. Severe light green (wild type)	*W* + *A*	*W*	Rapid
	W + *a*	*W*	Rapid
	W + *B*	*W*	Rapid
	W + *C*	*W*	Rapid
A. Mild light green	*A* + *a*	*A*	Rapid
	A + *B*	*B*	Very slow
	A + *C*	*C*	Slow
(*a*) Mild yellow			
B. Severe yellow	*B* + *C*		
C. Severe yellow			

When the mild-green mutant was paired with one of its direct mutants (a mild-yellow type) the mild-green virus dominated completely and almost immediately.

The results cited show that domination was not correlated with the relative degree of virulence, but was correlated with direct lineage, i.e. the green types quickly dominated their direct-line mutants regardless of colour reactions, but the severe yellow types which were derived immediately from the wild type slowly suppressed the mild-green type which was also an immediate derivative from the wild type, and dominance is still doubtful between the two severe yellow types (Table 1).

The basis for the relative degrees of domination manifested in the several mutants and the wild-type virus is not understood. We may be dealing with a type of antibiosis or with a particular type of protective action, or perhaps with a mechanism somewhat but not entirely similar to that which determines dominance and recessiveness in gene-controlled characters. However, the latter seems least probable since the dominant genes do not displace their alleles, but merely determine the character. Domination of the wild-type virus over all its mutants does suggest the situation in some of the eye-colour series of allelomorphs in *Drosophila* where the wild type dominates all of its mutants (Goldschmidt, 1938).

In another paper (McKinney, 1937) the writer referred to the common or wild-type virus used in his studies as the primary virus with respect to the mutants derived from it. However, it seems reasonably evident that all field collections of the wild type are not absolutely identical in all minor details, and it may be that the writer's wild type represents one of several slightly different mutants derived from another wild type not yet identified with this series.

The biological evidence now available indicates that the virus of tobacco common mosaic possesses the basic functions assigned to genes, i.e. it serves as a determiner of the specific reactions which make for its duplication (autosynthesis) and it mutates, forming a series resembling in certain particulars a series of allelomorphs derived from a wild type. These views seem not to impair the conclusions drawn from the chemical evidence that the virus is a parasitic nucleoprotein.

Muller (1922) suggested that bacteriophage virus may represent free genes. In a later paper Muller (1929) presented a strong case for the gene as the foundation of the first living matter, and Gulick (1938) views the genes as essentially living units. If the virus is living, what is its evolutionary history?

Oparin (1938) takes the view that "Natural selection has long ago destroyed and completely wiped off the face of the earth all the intermediate forms of organization of primary colloidal systems and of the simplest living things and, wherever the external conditions are favourable to the evolution of life, we find countless numbers of fully developed highly organized living things. If organic matter should appear at the present time it could not evolve for very long because it would be quickly consumed and destroyed by the innumerable microorganisms inhabiting the earth, water and air." In the light of our present knowledge of the tobacco mosaic virus Oparin's arguments lose some of their force. While this virus can be destroyed by certain microorganisms the fact remains that it stands high among biological entities with respect to its resistance to environmental factors as a whole. However, since many other mosaic viruses do not possess these high-resistance characteristics, we may be led to believe that the virus of tobacco common mosaic probably did not evolve for a very long period at least, outside a living cell.

Several investigators have suggested that the virus originates in a living cell. Lindegren (1938) postulated that an occasional gene released into the cytoplasm may increase there without restraint and thereby induce a diseased condition in the manner of a virus. If such a mechanism obtains in tobacco it would seem that finely pulped tissue of healthy tobacco plants should induce mosaic when intro-

duced into healthy plants, but such tests have failed to indicate that healthy plants are a source of virus.

In postulating the spontaneous origin of virus in a susceptible plant fewer difficulties seem to be encountered when we introduce mutation into the scheme. A gene, or some autosynthetic catalyst outside the chromosomes, perhaps in the cytoplasm, might mutate and thus give rise to a virus. Once formed the virus gene-molecule, endowed with a new set of catalytic forces, is ready to synthesize new molecules like its own. The "raw" materials, whether they be complex precursors and prosthetic groups or many simple precursor groups, must be in all healthy susceptible plants, but they cannot be brought into the right combination to produce a given virus until that virus is present. The subsequent mutations of the virus then introduce the new virus strains and possibly some non-virus catalysts as well. Perpetuation of a new virus strain is then made possible by a new catalytic force which effects a new combination of the groups already existing in the plant. If the virus represents a gene mechanism, then the postulated non-infectious autosynthetic catalyst would also represent one in the foregoing scheme.

Other possibilities also merit consideration. The virus may be a normal constituent in some vector or in some unrecognized symptomless plant species which serves as a source of supply for those species which manifest the pathological reactions, or it may represent a filterable phase of some micro-organism.

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MACKLIN, MADGE T. *An Analysis of Tumours in Monozygous and Dizygous Twins*

Although an analysis of tumours in twins does not yield information concerning the mode of inheritance of tumours, it gives valuable evidence as to the role of inheritance in tumour production. In a series of tumours in one or both twins, collected from the literature and from personal communications, the following results were obtained. Because the objection is valid that instances in which both twins are affected are more apt to be reported than those in which only one twin was affected, only those cases were selected in which both twins were affected. They were divided into the two classes, monozygous and dizygous, according to the statements in the reports. A third group, in which both twins were affected but in which no statement was made as to their being mono- or dizygous, was omitted. There were, up to date, thirty-eight pairs of monozygous twins, thirty collected from the literature, eight pairs collected through personal correspondence. Of these, thirty-six pairs were affected with the same type of tumour in the same organ, an incidence of 94·7 %. Two pairs, or 5·3 %, had different tumours. There were fifteen pairs of dizygous twins of whom seven, or 46·6 %, had the same type of tumour; and eight pairs, or 53·4 %, had dissimilar tumours. Thus agreement between twins of the monozygous type was more than twice as frequent as between twins of the dizygous type, even when the twins were selected on the basis of both being affected.

The difference between the ages of onset in the two classes of twins was studied also. In those cases in which age of onset of the tumours in the twins was given, the times elapsing between the age of onset in

the monozygous class was 15·5 months; in the dizygous class, 98 months or six times as long. Here again the monozygous twins tend to resemble each other more closely than do the dizygous twins, indicating that the age of onset is probably influenced by hereditary factors.

The series collected from the literature, and the series collected by correspondence in which the importance of reporting cases in which one twin only was affected as well as of reporting cases in which both twins were affected, agreed very closely.

The fact that there are records in which monozygous twins were not both affected, even after a long lapse of time, indicates that extrinsic factors play a role which may vary in importance in different types of tumours.

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McMeekan, C.P. and Hammond, J. ***The Relation of Environmental Conditions to Breeding and Selection for Commercial Types in Pigs***

The main differences between the bacon and the lard type of pig consist of the intensification of the early skeletal and muscular phase of growth in the former and the intensification of the subcutaneous fatty phase of growth in the latter. The commercial production of these two types takes place under quite different systems of farm management.

Within litters from the same inbred strain of Large White pigs individuals were made to grow along growth curves of predetermined shapes by controlling the plane of nutrition at different stages of growth.

By making rapid growth in the early stages (up to 16 weeks) and slow growth later the early developing tissues, such as skeletal framework and muscle, are intensified and the later developing tissues, such as the subcutaneous fat, are inhibited, thus producing the bacon type.

By making slow growth in the early stages (up to 16 weeks) and rapid growth later, the early developing tissues, such as skeletal framework and muscle, are stunted and the later developing tissues, such as the subcutaneous fat, are intensified, thus producing the lard type.

By controlling the nutritional environment so as to develop the character in question (muscular development or subcutaneous fat) to its physiological limit, it is possible to make proper genetic selection.

The way to improve our domestic animals for production, therefore, is to place them in the optimum environment for developing the character in question and select, preferably by means of the progeny test, those which show the development of the character in question to the fullest extent.

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McPhee, H.C. ***Recent Attempts to Co-ordinate Genetic Research on Farm Animals in the United States***

During the long period over which scientists have laboured in the laboratories of academic institutions since the rediscovery of Mendelism at the turn of the last century, a vast store of technical genetic information has been accumulated. Much of this information pertains to forms of life which have little or no relation to the livestock industry, yet the principles which have been developed as a result of this intensive research programme furnish the foundation from which one must start in the breeding improvement of farm animals.

Much has been written and perhaps more has been spoken on the value of genetic research in the livestock improvement programme, yet little has been done about it. We have seen during recent years the remarkable results of applying genetic principles to the improvement of various plants, notably corn, but there has not been a similar development in the animal field. It is always interesting to discuss the benefits which corn breeders have made possible, but to do this is only to waste your time because you already have heard the story several times.

From the experimental work with small laboratory animals, as well as the many experiments in the plant field, much has been learned about the effectiveness of different systems of breeding in controlling heredity. From the small-animal work we have learned the important fact that practically all of the characteristics of economic importance to the livestock breeder are affected by many inherent factors. Fertility, mortality, resistance to disease, growth, body size and type are to some extent controlled in their expressions by different inherent factors. We have learned further that many of these characteristics are inherited independently of each other. That is, a strain which is superior in some respect, such as for large body size, may be inferior in another respect, such as having low fertility. The simple process of long-continued close inbreeding which leads to the automatic fixation of hereditary factors has shown that strains can be developed which differ significantly in these respects. By use of selection during the inbreeding process it has been shown with rats that it is possible to maintain superiority in one or more characteristics such as size, but no genetic experiment has been carried on with either laboratory animals or farm livestock which gives a critical test of the limitations of improvement possible by intense inbreeding accompanied by selection and progeny test, and followed by intercrossing of strains. This is one of the missing links in the chain of genetic evidence in livestock improvement.

Attention has been given to one phase of this question recently by Goodale in his work on genotypic selection for size in mice. Starting with an unselected population in 1930 with the objective of determining the limit of change in body weight through selective breeding on a genotypic basis, Dr Goodale secured within sixteen generations some mice which were more than twice the average initial weight. The limits of possible increase are still undetermined.

Carrying such a technique over into the livestock field raises some interesting and important questions which must be considered carefully. In the first place, many of our breeds of livestock have been subject to more or less intense selection for a long period of years, and some of the possibilities of improvement, such as Goodale has secured in his mice, have already been realized. One must not overlook the fact, however, that most of our selection in livestock has been phenotypic and not genotypic, and therefore it is impossible to say what results will be obtained from a carefully conducted and similar experiment with swine, sheep or cattle. It is well worth trying.

Another important point centres around the variations which occur in our farm livestock. For the most part the mouse, the rat and guinea-pig vary very little in conformation, and when one animal is heavier than another it is usually larger all over in proportion. We know that this is not the case in some of our farm animals, such as swine, where great variation in type occurs. If one started selecting on a genotypic basis for weight alone he might end up with a large-type, heavy-boned, narrow-chested, slab-sided pig which would be practically worthless from the production standpoint. Similar statements might be made about other classes of livestock, and thus we see that the problem of genotypic selection when carried on with farm animals must consider more than one characteristic at a time.

As we all know, the pounds of milk and butterfat in the dairy cow, the number of eggs in chickens and the pounds of wool with sheep, are easily determined and recorded. They are mathematical expressions of the result of inherent producing factors, and by their use it has been possible to spot individual animals and strains which carry the inherent factors for high production. It is an interesting fact that there is a close association between the degree of genetic improvement in livestock and the availability of these exact measures of the product being improved. Thus we find that a great deal of progress in the development of high-producing dairy cows and of chickens has been realized by the breeder. Among the meat animals, such as swine, beef cattle and sheep, the situation is quite different, and here we find an almost complete lack of any exact measure or description of the characteristics of economic importance which it is desired to improve through the application of principles of genetics. This has been realized for a long time and has been pointed out repeatedly. It is to be regretted that progress in solving this important problem has been so slow. Animal husbandmen have placed their confidence in the show-ring standards because it was the only thing available. Among meat animals perhaps the show-ring procedure is not quite so worthless as it is for some other animals such as dairy cattle, because to some extent the conformation and meatiness of the animal are being judged and these are the characters which we want to improve. At best, however, it is only phenotypic in nature and is of relatively low order of value.

Recognizing the importance of having something more definite to record, we gave consideration three years ago to a project on the improvements of methods as the most important genetic project that could be put forward at that time for meat animals. Personnel has been at work in the Bureau of Animal Industry laboratories at Beltsville, Maryland, and in co-operation with State agricultural experiment stations in a comprehensive study on methods of recording data on meat animals which would be more useful to the animal breeder. Particular attention has been given to measuring variations in conformation, using both measurements and grading charts with photographic series for recording variations in conformation.

One of the important things which the accumulation of genetic information has made clear to us is that the essential genetic principles needed for the improvement of animals are already well known. It is not necessary to know how many genes are concerned in plumpness of hams, or what chromosome they are on before progress can be made. The work with the small laboratory animals involving hundreds of thousands of individuals bred for many generations of brother-sister mating, has shown that such close breeding automatically fixes heredity affecting many complex characters which go to make up the general vigour of a stock. It has shown also that one cannot always effectively direct the course of fixation by selection when the system of breeding is very intense. The large numbers, the long time and the expense involved are the factors which have prevented the geneticists from attempting similar work with farm livestock. However true this may be, a feeling has developed during recent years that only through some such attack can further advance be attained. This is the background which leads to the establishment of new organizations of effort to carry on experimentation in the breeding field of farm livestock. I refer specifically to the organization of the regional breeding laboratories.

The regional laboratories

The important stimulus to a new and intensive programme of experimentation dealing with the breeding improvement of livestock was furnished by the Bankhead-Jones Act of the 74th U.S. Congress, in 1935. This Act provides in part that "The Secretary of Agriculture is authorized and directed to conduct research into laws and principles of underlying basic problems of agriculture in its broadest aspect. One-half of such Special Research Funds shall be used by the Secretary for the establishment and maintenance of research laboratories and facilities in the major agricultural regions at places selected by him."

Following the passage of this Act nine regional laboratories have been approved and are largely organized. Only three of these are concerned with animal breeding: the Regional Swine Breeding Laboratory, the Western Sheep Breeding Laboratory and the Regional Research Laboratory for the Improvement of Viability in Poultry.

The major purpose of these laboratories is to bring about a better co-ordination of genetic research effort between the States and Federal Government. It is the hope that the pooling of funds and facilities, together with a concentration of genetic effort, will make possible the prosecution of long-time experimentation in which the newer concept of genetics will have an opportunity to demonstrate its worth in the improvement of farm livestock. These are more than genetics laboratories. In addition, they co-ordinate programmes in which the State and Government research workers in animal genetics are joining hands to apply the known principles of genetics for the express purpose of bringing about improvement.

Regional swine breeding laboratory

The first regional laboratory to be approved was the Regional Swine Breeding Laboratory with headquarters at Ames, Iowa. Twelve of the North Central States and Oklahoma are co-operating with the Bureau of Animal Industry in this undertaking. The main objective of this is the improvement of swine through the application of breeding methods. Improvement is being sought in productiveness of sows, growth of pigs, economy of gains, physical vigour and quality of carcass. To accomplish these objectives, use is being made of production recording and progeny testing in combination with various inbreeding and outbreeding systems. The need for new measures for use in selection is recognized and search is being made for more adequate measure of productiveness of sows, of variations in conformation and in carcass quality.

At the present time six of the co-operating States are actively engaged in carrying on breeding projects as a part of the laboratory programme. At these State stations a total of thirty-six separate strains is being developed by close breeding. There are twenty-three strains in the Poland China breed, ten in the Duroc-Jersey, two in the Hampshire and one from a Landrace × Tamworth crossbred foundation. Few of these strains have progressed far from the standpoint of increased homozygosis and no crossing of lines has yet been attempted. The first preliminary crossing of lines will be tried next year.

The Bureau of Animal Industry is carrying on simultaneously other breeding projects with swine at Beltsville, Maryland, and Miles City, Montana. While these projects are not a part of the Regional Laboratory, the two programmes are so co-ordinated that they supplement each other. At Miles City, Montana, the Landrace × Black Hampshire cross has been made on a scale which will furnish needed genetic information on various characters, besides establishing the basis for a new strain. At Beltsville, Maryland, similar crossing experiments are being carried on with the Landrace × Poland China, Landrace × Duroc-Jersey, Landrace × English Large Black and Yorkshire × Duroc-Jersey. All these crosses are carried either to the F_2 or backcross generations and in numbers approximating 150 for each cross. In addition, one inbred strain is being developed in each of the Danish Landrace, Duroc-Jersey and Poland China breeds.

Thus we have in the programme of the Regional Swine Breeding Laboratory and the Bureau of Animal Industry combined, a total of forty-four separate strains of swine being developed. Thirty-eight of these are confined to the so-called pure breeds and six have a hybrid foundation.

While it is not the intention to make a genetic study of swine it is hoped that as new things come to light as a result of the inbreeding there will be opportunity to follow through on the mode of inheritance and thus add to our knowledge of the genetics of swine. We believe that the co-ordinated programme provides opportunity for a sufficient number of lines and animals to guarantee, under the competent direction of genetic specialists, material contributions to our knowledge of genetics of swine and to the possibilities of improvement in the application of genetic principles.

Western sheep breeding laboratory

The second regional breeding laboratory to be approved was the Western Sheep Breeding Laboratory located on the site of the U.S. Sheep Experiment Station, near Dubois, Idaho, and conducted in co-operation with the twelve Western States, including Texas. The objective is to bring about breeding improvement for wool and lamb-producing qualities, using about the same scheme of close

breeding employed in the Regional Swine Breeding Laboratory. Of course with sheep it is not practical to use a uniform brother-sister type of mating in the inbreeding flocks, but there will be some parent-offspring, full brother-sister, half-brother-sister and other types of matings.

Because of its importance in the western range country, we have selected the Rambouillet breed as the starting point. Other breeds may be added to the programme later, but in the beginning we did not wish to retard the programme by adding several breeds and thereby cutting down the number of strains which could be carried. The first matings were made in the fall of 1937 and consisted of thirty-four pens of twenty-five ewes and one ram each, divided approximately equally among close inbreeding, moderate inbreeding, and the proving of sires. In the fall of 1938 the programme was expanded to make a total of sixty-four separate breeding pens.

While it is too early yet to report on results from these breeding tests the lambs obtained in the thirty-four pens comprising the first matings have a good indication of the possibilities involved in the method. Many of these pens were made up from purchased stock which possessed the most nearly ideal combination of desired fleece and body characters. Many different blood lines were represented in the different pens as well as in the ancestry of the individual sheep. It is not surprising, therefore, that the lambs show much variability in their wool and mutton characters. In many of the pens the segregation was so pronounced and so many undesirable characters segregated out that the pen had to be discarded. The most uniform lambs were obtained in the two pens made up of inbred stock produced on the U.S. Sheep Experiment Station. While the degree of inbreeding averaged only about 17% the pens contained individuals with a coefficient of inbreeding as high as 44%. The foundation stock for these two pens have been in the process of development for about eight years and indicate something of the possibilities of developing other closely bred strains possessing desirable characters.

While it was necessary at the start to purchase much stock without any breeding tests available, it is planned in the future to test sires by means of an inbreeding programme before new lines are started. Since acceptable breeding lines and proved strains can be developed through inbreeding they will be combined later to take advantage of hybrid vigour. It is probable that attempts will be made to produce three-way and double-hybrid as well as single-hybrid lines. Simultaneously an outcross scheme will be employed to test the value of the different strains in improving random-selected stock.

Extensive data are being collected on the characteristics of fibre and conformational characters of the sheep. As a supporting programme the Bureau is conducting special technical research on fibres at the Agricultural Research Centre, Beltsville, Maryland, and at a station at Fort Wingate, New Mexico, devoted to the study of south-western range and sheep-breeding problems. The results of research at these two points are made available through the Western Sheep Breeding Laboratory programme, and the three units are co-ordinated in such a way that they supplement one another.

As in the swine laboratory, the primary effort is the development of closely bred strains which can be later crossed and used to develop superior flocks. Our problem is not one of analytical genetics which would involve how the various characteristics are inherited, however important they may be. It is a problem in creative genetics involving by means of inbreeding a drastic reshuffling of the genes with the hope that through recombinations and hybrid vigour there will result a significant improvement in the sheep. At the present time, of course, we do not know whether this means relatively homozygous lines or a programme of controlled heterosis.

Regional poultry research laboratory

The third animal-breeding laboratory to be approved was the regional research laboratory for the improvement of viability in poultry, with headquarters at East Lansing, Michigan. The programme is conducted in co-operation with twenty-five of the North-eastern and North Central States.

An analysis of the problems facing the poultry industry to-day emphasizes the fact that the mortality problem, particularly among adult chickens, is of major concern. Although much field and experimental work has been carried on during past years we are still without adequate means of controlling many of the diseases of chickens. The fact that fowl paralysis is blamed for one-half of the annual loss of $100,000,000 from poultry diseases in the area covered by the twenty-five co-operating States, is perhaps the primary reason for selecting a programme sufficiently broad to permit investigation of all phases of fowl paralysis as the first essential.

The co-operative plan emphasizes a study of the pathologic and genetic aspects of fowl paralysis and the influence of different management practices, nutrition and parasitism. Among the major genetic and physiologic considerations which will receive early attention are: (1) the identification of susceptible and resistant strains; (2) determination of the effectiveness of breeding for resistance and susceptibility to fowl paralysis. Nutritional aspects of the problem are to be approached in so far as it is possible to determine the effect of different rations on the

incidence of fowl paralysis in stock of known genetic background. It is hoped that the pathologic aspect may be directed profitably toward histo- and chemical pathology, properties of the causative agent, and transmissibility. As with other diseases, the development of satisfactory diagnostic procedures is the foundation for effective control. Certainly the significance of such factors as heredity and environment cannot be appraised satisfactorily unless the characters and properties of the host as well as the etiologic agent are established within rather narrow ranges.

During the first year attention has been given to the construction of laboratory facilities, brooder houses, isolation houses, and laying houses required for the proper conduct of the work. Because of the nature of the problem, the physical plant had to be divided into two parts, one for the breeding and one for the pathological investigations, with adequate provisions for preventing the spread of infections. In the spring of 1939, approximately 1000 eggs were obtained from each of ten strains of White Leghorns and hatched at the laboratory. The chickens from each strain were divided equally into a control and a pathological group. Those in the pathological group were all inoculated with material from typical field cases of fowl paralysis. After these ten strains have been tested with respect to their resistance or susceptibility to fowl paralysis an effort will be made to increase the resistance and susceptibility of the most promising strains and families.

The programme of the laboratory will be closely integrated and correlated with those of the co-operating experiment stations so that results of progress will be freely interchanged to advance the programme without the usual lag between discovery and publication. Stock from the resistant and susceptible strains developed at the laboratory will be made available to the co-operating stations which are in a position to make tests on viability.

In addition to the regional laboratories for swine, sheep, and poultry, there has been organized a regional laboratory for the study of animal diseases with headquarters at Auburn, Alabama, and conducted in co-operation with thirteen of the southern States. The organization of these four regional laboratories by the Department of Agriculture on a co-operative basis with the State Agricultural experiment stations, brings to the fields of applied genetics and disease control an opportunity that has never existed before. Although progress to date has not been sufficient to publish results, all the laboratories have been organized and the work is definitely under way, on a scale which will guarantee significant results. It is hoped that by the time the next International Genetics Congress comes to pass there will be important contributions to offer.

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MADISSOON, H. ***Sur le caractère héréditaire de l'absence des deux reins***

L'organe de sécrétion de l'urine, c'est-à-dire les reins, passent, pendant la période de gestation, par trois phases successives de développement, qui sont conditionnées par l'hérédité. Quoique rarement, on a pourtant plusieurs fois constaté dans la littérature médicale des cas où les foetus à naître qui étaient privés d'un rein ou même des deux (aplasia renum). Les observations prouvent que de pareils cas sont également conditionnés par l'hérédité.

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MALÁN, M. ***Zwillingsuntersuchungen über die Orientierungsfähigkeit***

Verfasser hat an 40 eineiigen und 40 zweieiigen Zwillingspaaren zwecks Festellung der Vererbung der Orientierungsfähigkeit unter Modifizierung der durch Liebig ausgearbeiteten Methoden mit Ausschaltung des Sehvermögens räumliche Orientierungsversuche durchgeführt.

Zur Ausschaltung der eventuellen Geschlechts- und Altersunterschiede hat er in den einzelnen Altersgruppen gleichviele eineiige und zweieiige männliche und weibliche Zwillingspaare untersucht.

Durch dreimalige Untersuchung von 15 Zwillingspaaren hat er statt der Messung der individuellen Variabilität die Variabilität innerhalb der Paare bestimmt. Er hat so festgestellt, dass trotz der Grösse der intraindividuellen Variabilität die Paare bei wiederholten Untersuchungen konstante Abweichungen zeigen. Darum genügt zur Lösung der aufgeworfenen Frage eine einmalige Untersuchung.

Die Untersuchungen selbst haben ergeben, dass je nach welcher Richtung er die Versuche ausführte, die Abweichungen unter den Paaren sich verändern, jedoch in geringem Masse.

Ebenso verändern sich die Abweichungen bei den schwierigeren Versuchen, wo die Zahl der diskordanten Fälle bei eineiigen wie zweieiigen Zwillingen in gleichem Masse zunimmt. So kann das Orientierungsvermögen als stufenweise unterschiedlich angesehen werden.

Bei sämtlichen Versuchen zeigen die eineiigen Zwillinge kleinere Abweichungen innerhalb der Paare als die zweieiigen. Bei letzteren übersteigt die Zahl der extrem grossen Abweichungen vielfach die der ersteren.

Die Konkordanz der *eineiigen* Zwillinge ist sowohl

im absoluten Mass als auch prozentual wesentlich grösser als diejenige der zweieiigen. Diese Konkordanz ist mindestens doppelt so gross wie die Konkordanz der *Zweieiigen*. Natürlich ist die Diskordanz der letzteren eine vielfache der Diskordanz der eineiigen.

Auf Grund von all diesem kann die Erblichkeit *der Orientierungsfähigkeit* als bewiesen angesehen werden.

So ist *also die hervorragendere Orientierungsfähigkeit der primitiven Völker* nicht durch Übung und Anpassung also durch Umweltseinflüsse entstanden, sondern *ist eine durch erbliche Mutation entstandene und durch Selektion aufrechterhaltene Rasseneigenschaft.*

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MANGELSDORF, P.C. ***The Origin of Maize***

There have been three general theories regarding the origin of maize: (1) that it originated from pod-corn, *Zea mays tunicata*, which differs from normal maize primarily by a single dominant gene governing the development of a brittle, disarticulating rachis and the production of prominent glumes enclosing the seeds; (2) that maize originated from teosinte, *Euchlaena mexicana*, by direct selection, by large-scale mutations or by the hybridization of *Euchlaena* with a grass now unknown; (3) that *Zea*, *Euchlaena* and *Tripsacum*, the three American Maydeae, have descended along divergent and independent lines from a remote common ancestor.

New evidence from cytogenetic studies at the Texas Experiment Station suggest that *Euchlaena* has had no part in the ancestry of maize, but is instead the product of natural hybridization of *Zea* and *Tripsacum*. *Euchlaena*, which is intermediate between *Zea* and *Tripsacum* in many characteristics, differs genetically from *Zea* primarily by four segments of chromatin, all of which have genes with *Tripsacum* effects. Hybrids of *Zea* and *Tripsacum* have shown that there is some association between chromosomes of the two genera and that interchanges of chromatin may occur. The combined data agree in pointing to the comparatively recent origin of *Euchlaena* as the result of natural hybridization of *Zea* and *Tripsacum*.

With *Euchlaena* eliminated from a role in the origin of maize, it is reasonable to assume that maize originated as a mutation from a wild pod-corn once indigenous, and perhaps still to be found, in the lowlands of South America. The primary centre of domestication probably occurred in the Andean region of Peru and Bolivia. Historical and archaeological evidence supports this view.

The hybridization of *Zea* and *Tripsacum* which occurred when the two genera were brought into contact with each other in Central America gave rise not only to the new genus *Euchlaena*, but to new forms of maize which spread in both directions, almost completely replacing pure maize in all regions except the Andean. Cytological evidence on chromosomal knobs supports the view that almost all modern maize varieties are contaminated with *Tripsacum*.

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MANN, C.E.T. ***Improvement of Yield in* Hevea brasiliensis**

It is shown that by breeding between selected parents seedling families may be obtained whose average yields are equal to those of budded trees of the best clones. Variation within legitimate seedling families is considerable. This is illustrated by reference to data from selected seedling families.

Applications of the results of breeding work to practice are described, and a brief account is given of the measures adopted to obtain large quantities of seeds of good parentage by the establishment of special areas for seed production.

The relative merits of budded trees and seedlings in practice are discussed. The practical advantages of uniformity of budded trees are contrasted with the disadvantages of variation which is encountered in all seedling families which have been obtained so far. It is shown that characters, other than satisfactory latex-yielding properties, are of great practical importance.

Variability within high-yielding seedling families is of considerable importance in that it gives further opportunities for the successful application of the vegetative method. New clones made from selected individuals of some of the early crosses have already been tested. Many of these new clones appear to be superior to the older clones and are capable of higher average yields than the families from which they have been derived.

It is suggested that for the present the vegetative method offers the best means of providing adequate supplies of improved material for planting. Considerable further advances may be made by combining the vegetative method of propagation and distribution with further selection and carefully planned breeding work.

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MANRESA, M., REYES, N.C., GOMEZ, F., ZIALCITA, L.P. and FALCON, P.R. ***The Influence of Atmospheric Temperature upon Haemoglobin and other Constituents of the Blood of Cattle***

As in other tropical countries, pure-bred stock imported from temperate climates proved unsuited to the local environment. Haematological studies were begun in 1930 in the attempt to discover causes of the non-adaptability; haemoglobin determinations could be used as guides in evaluating adaptability (Manresa and Reyes, 1934). The following haemoglobin indices (g. per 100 ml.) were found: Philippine native $9{\cdot}43 \pm 0{\cdot}13$; Indian Nellore $9{\cdot}87 \pm 0{\cdot}09$; American Hereford and Holstein-Friesian $6{\cdot}76 \pm 0{\cdot}11$ and $6{\cdot}88 \pm 0{\cdot}17$ respectively; cross-breds were intermediate. The figures for the Friesian are significantly lower than those reported for the same breed in U.S.A. (Brooks and Hughes, 1931; Neal and Becker, 1933); this is explained on the basis of environmental temperature effects. Investigations on Nellore oxen showed a negative correlation between haemoglobin index and atmospheric temperature throughout the day, and also that the index was higher during the cooler months of December, January, and February, than in the summer. In animals already acclimatized (e.g. Nellores in the Philippines) fluctuations in blood composition occur without serious effect on constitutional vigour. Investigations on pure-bred Holstein-Friesian, pure Indian Nellore, and F_1 hybrids showed that haemoglobin, number of erythrocytes, specific gravity of blood, and the serum phosphorus-calcium ratio were positively correlated to adaptability to temperature; while uric acid, serum phosphate and size of red blood cells were inversely correlated.

Body temperature of Holsteins side by side with Nellores and F_1 hybrids was consistently higher, the figures during an eight months' study being 39·5, 38·7 and 38·7° C. respectively. Atmospheric humidity acts as a contributory factor to temperature; with air temperature at 24·9° C., a reduction in relative humidity from 82 to 75 % causes a fall in body temperature in the Holstein (in one case from 40·1 to 39·2° C.). No similar effect was observed in the Nellore. The mean annual temperature in the Philippines is 26·6° C., with average monthly maxima of 33·9° C. Regan and Richardson (1938) have shown marked accelerations in respiratory rate with increased temperatures in Holsteins, Jerseys and Guernseys. It is concluded that temperature is the most important limiting factor in the Philippines affecting the success of importations, since high air temperature raises body temperature, the normal physico-chemical balance of the blood becomes greatly disturbed, and the changes operate adversely on the general constitution, making the animal incapable of adjusting itself to the new environmental conditions. High atmospheric relative humidity, in retarding evaporation and cooling, aggravates the effect of air temperature.

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MANTON, IRENE. ***Evidence on Chromosome Structure in* Osmunda**

As a result of the study of spiral structure in mitosis and meiosis in one plant, it has been possible to demonstrate the existence of "long-range elasticity" in the chromosome thread and also to show significant changes of chromosome length in the meiotic, as opposed to the mitotic, prophases. A molecular interpretation is suggested.

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MARCHLEWSKI, T. ***Indication of Sex-linkage in Milk-yield Inheritance in Cattle***

The following observations were made in a highly inbred herd of Red Polish cattle with an average inbreeding coefficient of 19·48 %. The stock bull responsible for most of the subsequent inbreeding from sire × daughter mating, was found to increase slightly the yield of his daughters. His productivity index of 3800 kg. with 4·66% butter-fat lies above the herd average of about 3350 kg. with 4·22 % butter-fat. As the sire and grandsire of this bull had a productivity index of but 2200 kg. with 4·40 % butter-fat, and had a decidedly deteriorating influence upon the yield of the entire herd, the positive properties of the stock bull "Juras III" are undoubtedly due to the influence of his female ancestry. The average yields of the dam and granddam were 4200 kg. ± 4·10 % and 4400 kg. ± 4·70 %, respectively. It was found that, on the average, though the amount of inbreeding rose in some instances to 37·5 %, the milk yield was dependent in the first place upon the initial performance of the females in tail female line from the foundation stock of the herd. "Good" families remained, on the average, more productive, and "poor" families rather less efficient. The sons of "Juras III", widely used in the whole of the Red Cattle breeding area, showed very great variation in their productivity indices, from directly detrimental to undoubtedly positive. Here a decided relation between the performances of the bulls studied and the yield of their dams was apparent. A statistical analysis of the data strongly suggests sex-linkage in milk-yield inheritance, though the evidence is unfortunately rather scanty numerically.

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MARCHLEWSKI, T. *Change of Dominance in Canine Colour Genetics*

The writer reports on the results obtained in crosses of the Australian dingo and black and tan Scotch collies.

Present and previous results show that a number of modifying factors are present in the dingo, accumulated in the course of selective processes, which change the order of dominance from black towards yellow.

Certain domestic breeds seem to have undergone a similar process in the course of a relatively short period of time.

On crossing yellow F_1 dingo × collies with suitable yellow domestic dogs, in agreement with expectation, a black phenotype was obtained. This phenotype enables the study of the specific action of certain of these modifiers, isolated from the complicating effects of others. Thus it was found that a practically new colour, dark sooty brown, is due to the isolated action of a yellow enhancer with a highly penetrating effect, that a "mock" black and tan pattern may be produced as the effect of other genes of this order, and so forth.

The results are discussed in the light of Fisher's theory, and regarded as instances confirming this conception.

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MARSHAK, A. *Chromosome Structure in Meiosis and Mitosis*

The survival curves for all the chromosomes studied is of the form $Y = e^{-kx}$, indicating that the observed effects are produced directly by the X-ray ionization and not by the intervention of a toxic substance. The slopes vary directly with the length of the chromonema, which indicates that the cross-sectional area of the sensitive material is approximately of the same size in the species studied and has a diameter of 10^{-7} cm. This calculation is made on the assumption that each ion pair is capable of producing an alteration leading to a chromosome abnormality.

To test this assumption the effects of neutron bombardment on the same species was investigated. The stage of maximum sensitivity was the same as with X-rays, and the survival curves were all exponential. Again the slopes varied directly as the lengths of the chromonemata. In each case the slope is 2·6 times that of the X-ray slope, assuming that each unit n of neutron ionization is equivalent to 2·5 röntgen units which seems to be the best evaluation of the n unit. Thus, the cross-sectional areas of the sensitive volume must be approximately the same in all species, for otherwise the ratio of neutron slope to X-ray slope would vary. Further, the diameter of this area must be of the order of 10^{-7} cm. or less, or the neutron ionization would be much less efficient than X-rays. The factor 2·6 does not rule out the possibility that a single ion pair may produce a chromosome abnormality. The diameter of the sensitive volume from X-ray data may represent only a minimum value for the size of the structure responding. The neutron experiments set an upper limit which corresponds in order of magnitude with the value obtained with X-rays.

Chromosomes in the resting nucleus have two visible, well separated chromonemata. From the fact that the maximum abnormalities are observed in the first anaphase after irradiation it was postulated that the chromonemata which divided at the end of the resting stage were disjoined in the following anaphase. The hypothesis is supported by counts made of the frequency of "chromatid" and "chromosome breaks" at various intervals after irradiation. The data obtained by other investigators which conflict on other theories concerning chromosome division fit this hypothesis quite well and are not mutually contradictory. It is also supported by observations made on half-chromatid fragments. The latter reach a sharp maximum in frequency at 18 hr. after irradiation. Of thirty-six pairs of such fragments studied, all could be seen to come from *disjoining half-chromatids* which had deficiencies of corresponding size.

The abnormalities produced by X-rays in pachytene of the reduction divisions of *Vicia faba* pollen mother cells (observed in anaphase 24 hr. after irradiation) is an exponential function of dose. The slope of the curve is almost exactly the same as that for somatic mitosis. Such equivalence is to be expected if all four chromatids approach to within molecular distance, if only homologous chromatids are closely paired and each has a cross-sectional area equal to that of the somatic chromosomes at the end of the resting stage prior to division.

196

MATHER, K. *Selection for Polygenic Characters*

The most important characters of crop plants are polygenic in inheritance. Selection for such characters would be much facilitated by a detailed knowledge of their hereditary behaviour. Study of such characters is complicated by their variability being dependent on both genotype and environment, and also by the lack of a simple correspondence between genotype and phenotype. Statistical analysis is necessary to

overcome these difficulties. Suitable methods are now available; covariances and third degree statistics are especially valuable.

Recent work on this question has been concerned especially with (1) the dominance relations of the genes, (2) their interaction, (3) the effective number of genes, (4) the effects of linkage.

It has been commonly assumed in the past that all the genes involved in the control of one character show the same dominance relations. There is no *a priori* reason for such an expectation. Indeed, there is some reason for believing that, in unselected material, roughly equal numbers of genes show dominance in the two directions, plus and minus. In selected material, such as commercial plants, this equality of dominance may be upset, the larger number of segregating genes showing dominance in the direction of selection. Thus selective advance becomes more and more difficult.

The manner of interaction of the genes is of less interest, apart from questions of epistasy, as it will usually result solely in metrical skewness of the curves. Though selection may appear to be more difficult in one direction, this is not because of the absence of desirable segregant types but because the metrical scale is, so to speak, foreshortened in that direction.

With a knowledge of the number of genes involved in a segregation more accurate predictions of selective advance can be made.

The main effect of linkage seems to be in "damping" the observable variability of polygenic characters. There will be a balance of plus and minus genes in each chromosome, and the value of such a balanced complex should be less variable than the effects of the constituent genes. The first effect of selection will be to select out the best combinations of chromosomes, but provided some heterogeneity is maintained, advances may also be obtained as a result of the chromosome balances being broken up by crossing-over. Such advances may be more striking than those which depend on a reassortment of the chromosomes one with another.

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MATTHEY, R. ***The Problem of Heterochromosomes in the Reptile***

Neither in birds nor in Amphibia have sex or heterochromosomes showing morphological differences in the digametic sex, been yet observed. Such heterochromosomes are characteristic of the male sex in mammals. Further evidence was obtained, by analysing the chromosome complements of the parrot and budgerigar, that the digametic sex is the female, and that the sex-determining mechanism is of the *XO* type. Recent studies on the lizard, viper and chameleon have similarly shown that in the reptiles the female is the digametic sex. These observations are contrary to previous findings, according to which the reptiles are characterized by male heterogamety.

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MAZIA, D. and JAEGER, L. ***Nuclease Action, Protease Action, and Histochemical Tests of Salivary Chromosomes of*** **Drosophila**

Although there the evidence is clear for the presence of both proteins and nucleic acids in salivary chromosomes, it is incomplete (*a*) on the nature of the proteins, (*b*) on the continuity of the protein through the euchromatic and heterochromatic regions, (*c*) on the role of nucleic acids in the architecture of the chromosome.

In the present experiments, these problems are attacked by treating salivary material with enzymes specific for proteins and for nucleic acids, and observing their effects on the chromosomes by histochemical methods specific for proteins and for nucleic acids. Pepsin, crude trypsin, and crystalline trypsin were used as proteolytic enzymes, and a nucleic acid-splitting enzyme solution was prepared from beef spleen. Nucleic acid was demonstrated by the Feulgen reaction, protein by the ninhydrin test. Tests were carried out at 37° C. and thymol was used to prevent bacterial action. Whole fresh glands were treated.

As Caspersson had found, trypsin causes the complete disintegration of the chromosomes: 3–4 hours' treatment suffices. In controls treated with boiled samples of the trypsin solution structure remained normal. Pepsin, on the other hand, did not completely digest the chromosomes. After pepsin treatment (3–30 hr.) the chromosomes were still present and stainable, but appeared shrunken when compared with controls. Since protamines and histones are completely digested by trypsin but not by pepsin, it is quite possible that these proteins are concerned in maintaining the structure of the chromosomes, and are continuous through the light and dark bands. An alternative possibility is that nucleoproteins (which are not digested completely by pepsin) form a continuous framework through the chromosome, though their concentration in the heterochromatic bands is very low.

Treatment with spleen nuclease (probably a mixture of nucleic acid splitting enzymes) did not affect the integrity of the chromosomes. They could not, however, be demonstrated by the Feulgen or the aceto-carmine technique. On the contrary, these techniques, after nuclease action, produced an intense staining of

the cytosome. But the chromosomes could be stained by means of ninhydrin, the protein reagent. Chromosomes in boiled nuclease behaved normally.

It is concluded (*a*) that chromosomes contain a continuous protein framework, (*b*) that the architectural proteins may be protamines or histones, although an alternative interpretation is possible, and (*c*) that the structural integrity of the chromosome is independent of the presence of intact nucleic acid molecules. The latter point contradicts the hypothesis of Wrinch.

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MELCHERS, G. ***Neuere Untersuchungen über die Physiologie der Genwirkung an Pflanzen***

Die möglichst lückenlose Erfassung der Reaktionsketten, welche im Verlaufe der Ontogenie vom Gen zum fertigen Merkmal führen, ist die wesentlichste Aufgabe der Entwicklungsphysiologie. Die auf verschiedener genetischer Konstitution beruhenden Unterschiede in den Blütenfarben und ihren Mustern konnten mehrfach auf chemische Beziehungen der Farbstoffe untereinander und zu ihren ungefährbten Vorstufen zurückgeführt werden (Lawrence und Scott-Moncrieff, 1935; Scott-Moncrieff, 1936, 1937, 1938; Beale, Robinson, Robinson and Scott-Moncrieff, 1939; Störmer und v. Witsch, 1937). Die in diesen Arbeiten erschlossenen und zum Teil erfassten biochemischen Reaktionen sind wohl alle am Ende der Reaktionskette vom Gen zum Merkmal einzuordnen. Sie betreffen in diesen Fällen unabhängig-zelluläre Differenzierungen. Dass aber auch innerhalb der Zelle bei der Differenzierung des Plasmas unter dem Einfluss des Kerns hormonartige Wirkstoffe in der Reaktionskette eine Rolle spielen, wurde von Hämmerling (1934) mit Transplantationen zwischen kernhaltigen und kernlosen Stücken der Riesenzellen von zwei *Acetabularia*-Arten gezeigt. Went (1938) konnte durch Transplantation Merkmale einer *Pisum*-Rasse deneneiner anderen annähern. Die genetischen Unterschiede zwischen den Transplantationspartnern sind in den beiden letzten Fällen zwar nicht genauer bekannt, der Schluss, dass die nachgewiesenen Wirkstoffe ihren Platz irgendwo zwischen Genom und Merkmalen haben, ist aber wohl statthaft. Einen Nachweis hormonal-abhängiger Differenzierung bei bekannter monohybrid verschiedener genetischer Konstitution erbrachten v. Wettstein und Pirschle (1937), Pirschle (1939) bei *Petunia*. Ein Teil der Merkmale, vor allem der mit fortschreitendem Alter stärker werdende Chlorophyllschwund der Mutante "*defecta*" liess sich im Transplantationsversuch auf die normale Sippe übertragen. Über zwei ähnliche Fälle berichtet Stein (1939). Eine Tomatenmutante "*nana*" wurde im Wuchs der Ausgangsrasse angenähert, wenn sie auf diese gepfropft wurde. Die unter den gegebenen Versuchsbedingungen nicht blühfähige Mutante "*sterilis*" von *Antirrhinum siculum* konnte nach Transplantation auf normale, blühfähige Unterlagen unter sonst gleichen Bedingungen zum Blühen gebracht werden. Daraus wurde auf die Wirkung eines zwischen dem +-Gen und der Blütenbildung eingeschalteten Blühhormons geschlossen.

Nur durch ein Genpaar unterscheiden sich auch die einjährige und die zweijährige Rasse von *Hyoscyamus niger* (Correns, 1904). An diesem Objekt gelang es zum ersten Mal bei Pflanzen, durch Transplantation die eine Rasse durch die andere zu beeinflussen (Melchers, 1936, 1937). Als Wirkstoff wurde ein Blühhormon angenommen. Es kann aber kaum ein direkter Zusammenhang zwischen dem die Einjährigkeit bedingenden Gen *ann* und dem Hormon im Sinne eines "Genhormons" bestehen. Denn $\frac{+ann}{+ann}$-Pflanzen (zweijährige) kommen auch zum Blühen, wenn ihre Vegetationsspitzen tiefen Temperaturen ausgesetzt werden. Einen ähnlichen, wahrscheinlich indirekten Zusammenhang zwischen Gen und Hormon konnte van Overbeek (1938*a*, *b*) bei *Zea Mays* feststellen. Der *nana*-Wuchs einer Mutante konnte auf grössere Auxin zerstörende Fermentaktivität des *nana*-Gewebes zurückgeführt werden. Der Mutante "*lazy*", welche eine niederliegende Wuchsform hat, fehlt die Fähigkeit, bei Horizontallage der Sprosse, das Auxin auf die Unterseite zu verlagern.

Für die Entwicklungsphysiologie der Blütenbildung ist es wichtig, dass die Existenz zweier verschiedener Hormone wahrscheinlich gemacht werden konnte. Čajlachjan (1936, 1937), Kuijper und Wiersum (1936) und vor allem Moschkov (1937) haben unabhängig von den Versuchen mit ein- und zweijährigen Pflanzen durch Transplantationen zwischen Kurztag- und Langtagpflanzen erstere entgegen ihrer genetischen Konstitution zum Blühen bringen können, und haben daraus ebenfalls auf die Existenz eines Blühhormons (*Florigen*) geschlossen. Es konnte wahrscheinlich gemacht werden, dass diese mit verschiedenen Tests nachgewiesenen Hormone nicht identisch sind (Melchers, 1938, 1939), denn die Kurztagpflanze *Nicotiana Tabacum* "Maryland Mammoth" (M.M.) brachte in Langtagbedingungen, in denen sie selbst frei von Florigen sein muss, $\frac{+}{+}$-*Hyoscyamus* zum Blühen. M.M. muss also schon in Langtagbedingungen ein anderes Hormon enthalten, welches die Einjährigkeit bedingt (*Vernalin*). M.M.-Pflanzen werden in Langtagbedingungen durch Transplantate

von $\frac{ann}{ann}$-Pflanzen zur Blüte gebracht, denn *Hyoscyamus niger* ist eine Langtagpflanze und bildet daher Florigen. Mit $\frac{+}{+}$-*Hyoscyamus*-Transplantaten, welche noch kein Vernalin enthalten, kann man wahrscheinlich M.M. in Langtagbedingungen nicht zum Blühen bringen (Melchers, unveröffentlicht). Daraus darf geschlossen werden, dass Florigen erst gebildet werden kann, wenn Vernalin anwesend ist. Wir können unsere derzeitige Arbeitshypothese für das Zusammenwirken der Hormone, welche die Blütenbildung veranlassen, in folgendem Schema zusammenfassen:

I. Vorstufe ⟶ Vernalin ⟶ Florigen

II. Vorstufe_V ⟶ Vernalin ↓

Vorstufe_F ⟶ ⟶ Florigen

Zwischen den Möglichkeiten I und II kann natürlich derzeit in keiner Weise entschieden werden. Auch ist noch nicht mit Sicherheit zu sagen, ob vom Gen *ann* irgendeine fördernde Wirkung auf die Umwandlung der Vorstufe ausgeht, oder ob das Gen $+^{ann}$ die Entstehung des Hormons aus der Vorstufe hemmt.

Die botanischen, entwicklungsphysiologischen Untersuchungen kommen demnach zu ähnlichen Ergebnissen wie die entsprechenden zoologischen Analysen, vor allem an Insekten. Von Genhormonen in diesem Zusammenhang zu sprechen, erscheint mir für unsere Fälle noch verfrüht, denn entweder sind die genetischen oder die physiologischen Analysen noch nicht weitgenug durchgeführt, um einen direkten Zusammenhang zwischen Gen, Hormon und Merkmal zu beweisen, oder es konnte sogar nachgewiesen werden, dass ein solcher direkter Zusammenhang sehr unwahrscheinlich ist. Da wir aber erst im Anfang dieser Forschung stehen, können wir noch auf schöne Erfolge rechnen, vor allem, wenn die neuen Hormone in wirksamen Extrakten vorliegen. Für einen der für die Blütenbildung wichtigen Faktoren hat H. Ullrich soeben mitgeteilt, dass ihm die Extraktion aus Crocusnarben gelungen ist.

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v. WETTSTEIN, F. und PIRSCHLE, K. (1937). *Biol. Zbl.* **58**, 123.

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MENSINKAI, S.W. *Evolution in the Genus* Allium

Seventeen species of *Allium* (fifteen for the first time) comprising eleven diploids, four tetraploids and two hexaploids have been cytologically studied.

The genus is divided into six sections mainly after Regel, and the line of evolution in each section and in the genus as a whole is discussed.

Evolution in the genus is taking place along three lines: (1) change in the number of chromosomes, (2) change in their structure, and (3) change in the genotype.

Change in number is towards polyploidy, aneuploidy and polysomy which are partly due to univalent formation. Five species, *A. Cepa* ($n=8$), *A. sewerzowii* ($n=8$), *A. nigrum* ($n=8$), *A. Scorzoneraefolium* ($n=7$), and *A. Bidwelliae* ($n=14$), show univalents whose behaviour is described.

All the polyploid species studied appear to be allopolyploids; polyploidy has arisen by duplication of chromosome sets after interspecific hybridization. Duplication is proceeding along three apparent basic numbers, 7, 8 and 9. Of these no. 8 seems to be the most primitive, and the derivation of 7 and 9 from 8 is discussed.

A. Cepa and *A. sativum* appear to be secondarily balanced diploids each with two pairs of nucleolar chromosomes and two pairs of nucleoli.

All the known structural changes except deletion are observable in the species investigated. Of these, inversion heterozygosity has played a prominent role in species differentiation. Six species, *A. Cepa* ($n=8$), *A. sewerzowii* ($n=8$), *A. cilicicum* ($n=8$), *A. Scorzoneraefolium* ($n=7$), *A. nigrum* ($n=8$) and *A. Bidwelliae* ($n=14$) show inversion. Fragmentation, fusion and reciprocal translocation are less frequent.

Genotypic changes have brought about a decrease in size of the chromosome complement in *A. decipiens* ($2n = 16$) and *A. cyaneum* ($2n = 32$), and an increase in *A. margaritaceum* ($2n = 32$).

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METZ, C.W. ***Species Hybrids, Evolutionary Chromosome Changes, and the Mechanism of Chromosome Rearrangement in*** **Sciara**

The present opportunity for interchange of ideas on current problems has led me to choose for discussion a subject which deals with investigations not yet finished and with questions not yet answered. I wish to consider the detailed nature of evolutionary chromosome changes—a field in which new possibilities were recently opened up by the discovery of the salivary gland chromosomes of Diptera through the well-known work of Heitz and Bauer, Painter, King and Beams, and Kostoff. A striking example of what can be done in this field is provided by the brilliant studies of Dobzhansky and his co-workers on *Drosophila pseudoobscura* and its close relatives.

Obviously, it is desirable to extend investigations of this kind to other groups of Diptera than *Drosophila*, and especially to groups not too closely related to *Drosophila*. For such a purpose the genus *Sciara* provides excellent material, both because of its inherent suitability, and because our previous studies have laid the necessary foundation of knowledge concerning the genetic behaviour and cytological characteristics of several species (Metz, 1938*a*). It is with the results of our recent work in this genus that the present account deals. The investigation has been greatly facilitated by the cordial co-operation of Dr Dobzhansky, who has made invaluable suggestions from his experience with *Drosophila*. For a more general discussion than is possible here reference should be made to Dobzhansky's book, *Genetics and the Origin of Species*.

Our immediate problem is to determine to what extent conditions in *Sciara* agree with those in *Drosophila*, and to inquire into the significance of the similarities and differences. The main topics considered are: (1) the nature of spontaneous chromosome changes which occur either within a species or during the differentiation of two species from a common ancestor, and (2) the mechanism of chromosome change.

CHROMOSOME CHANGES OCCURRING IN NATURE

A. Conditions in Drosophila. The studies of Dobzhansky (see Dobzhansky, 1937), of Sturtevant and Dobzhansky (1936) and of Dobzhansky and Tan (1936), on *D. pseudoobscura* and its relatives, will long stand as models for future work. They have shown that in this material, (1) the common type of spontaneous chromosome modification is an inversion of a chromosome segment, either large or small (twenty-eight were found in wild strains of *pseudoobscura*), (2) translocations of chromosome segments between non-homologous chromosomes, and also small localized changes which show as "deficiencies" of one or a very few disks, are detected rarely, if at all, within individual species, but are revealed in small numbers in hybrids between *D. pseudoobscura* and *D. miranda*, and (3) in the latter hybrids there are certain chromosome regions in which homologies are not evident, presumably because of complex rearrangements.

Other investigators find similar conditions in other species, and hybrids, of *Drosophila* (see e.g. Dubinin, Sokolov and Tiniakov (1936), Frolowa (1936), Kaufmann (1936), on wild strains of pure species; and Patau (1935), Kerkis (1936), Horton (1939), Hughes (1939), on hybrids). Of special note is the frequency of inversions and the rarity of minute "deficiencies", both within individual species and in species hybrids, in *Drosophila*. The rarity of minute "deficiencies" is verified by unpublished observations of Dobzhansky on *D. pseudoobscura* and *D. miranda*, and of Bridges on *D. melanogaster*, which I am permitted to cite.

It may also be noted that spontaneous inversions are apparently frequent in another dipteran genus, *Chironomus*, as Bauer (1936) has shown, and as we have observed in American material (unpublished).

B. Conditions in Sciara. In *Sciara*, conditions seem to be almost the reverse of those just described. The spontaneous inversions and translocations found commonly in *Drosophila* have not been detected at all, with the exception of one or two possible inversions; whereas minute, localized "deficiencies" are relatively common, not only in hybrids but within individual species. A few "repeats", of a few disks each, have been found in *Sciara*, as in *Drosophila*, but so far as known they are symmetrical and uniform throughout each species. They involve transpositions, of course, but not reciprocal translocations.

In wild strains of *Sciara ocellaris* at least seventeen cases of minute "deficiencies" have been found, including representatives in each of the four chromosome pairs. Similar cases have been found in *S. coprophila* and *S. impatiens*, of which only a few specimens have been studied. None has been found in *S. reynoldsi*, possibly because here also only a few specimens have been examined. This class of modifications apparently includes two kinds. One involves what may be a true deficiency of a disk, or a pair or small cluster of disks (see loci 5 and 6 in Fig. 2, from a hybrid; also see Metz, 1937, 1938*b*). No adjacent

similar structures are found here. If the missing disks are present elsewhere in the chromosome, or haploid group, they have not been detected; and no synapsis has been observed between the extra disks and any others. In the second kind, the extra disk or small cluster in the one homologue lies next to a similar disk or cluster which extends across both homologues (see Figs. 3 and 4, from a hybrid). Here the single band or cluster in the deficient homologue may sometimes connect with both bands in the other (Metz, 1937, Figs. 2, 3, 4, 10). This kind, therefore, has the appearance of a duplication, as if the band or cluster had doubled. If that is the case, it represents an addition rather than a loss.

It has been shown that these minute modifications are persistent over many generations, both in nature and in the laboratory; but no external morphological characters have yet been associated with any of them.

In hybrids between *S. ocellaris* and *S. reynoldsi* a comparable situation is found. Four chromosome pairs are formed, symmetrical as to length and general pattern. No inversions or translocations have been detected, although the patterns have been homologized in all but a few relatively short regions. Numerous minute modifications are found, like those just described in *S. ocellaris* (Figs. 2–4). Judging from the few regions examined in fine detail there are probably from thirty to fifty or more such minute alterations in the hybrid, including both kinds.

In the hybrids, minute differences are found at the ends of all four chromosomes, which suggests that modifications occur at or near the tips with relatively great frequency. A similar interpretation may be given to Horton's findings in hybrids between *Drosophila melanogaster* and *D. simulans*, where four of the ten known modifications are at chromosome ends (see also Kikkawa, 1938).

In addition to the "minute" modifications there are found in the hybrids a few cases of larger modifications. The nature of these is not yet clear, but no evidence has been found to indicate that they represent inversions or translocations. It seems probable that they are large duplications.

Certain characteristics of two chromosome pairs (*C* and *X*) call for special consideration. As shown by Crouse (1939) the metaphase chromosome groups of *Sciara ocellaris* and *S. reynoldsi* are alike, except for the shape of one chromosome pair, which is V-shaped in *reynoldsi*, but may consist of two V's, two rods, or a rod and V in *ocellaris*. The size is uniform throughout. The interesting fact here is that in heterozygous individuals of *ocellaris* the V and rod exhibit complete, close pairing, with no evidence, thus far detected, of an inversion or other asymmetry. Curiously enough, although this chromosome behaves "normally" in both ordinary mitotic cells and salivary gland cells in *ocellaris*, its supposed counterpart (chromosome *C*) in *reynoldsi* does not. In the salivary glands, but not in mitotic cells, of *reynoldsi*, it breaks into two segments during development and often appears as two short chromosomes. The same feature is shown in the hybrids, where the pieces associate with the corresponding parts of the *ocellaris C* (Fig. 5).

The *X*-chromosome, in both *ocellaris* and *reynoldsi*, usually appears in the form of a figure 8, due to the presence of what is interpreted as a triple "repeat" involving at least three or four disks (Fig. 1; also Metz, 1935, Frontispiece; and Metz and Lawrence, 1938, Figs. 10, 13). This causes the two ends and a region near the middle of the chromosome to be attached together. These repeats appear to be just alike, and in the same relative positions, in the two species; hence they apparently have persisted unaltered during the evolution of the two species from a common ancestor. The case suggests some interesting speculations regarding persistence of genic materials and regarding synaptic forces in hybrids as compared with pure species, but these cannot be treated here.

Possible qualitative changes

It is generally agreed, I believe, that regardless of what particular theory of evolution one holds, or of the types of quantitative chromosome changes observed, it is necessary to assume the occurrence of qualitative changes in the genic materials. For this reason special attention has been given in the present studies to cases in which morphological differences might be interpreted as indicating the presence of qualitative differences between homologous loci. One such case is found near end 1 of chromosome *B* in the hybrids between *S. ocellaris* and *S. reynoldsi*. The general region in question appears to correspond in the two species, as indicated both by the likeness in pattern and the paired association. At one "locus" or short section within this general region, however, the pattern in the *reynoldsi* chromosome is typically made up of sharp bands or disks, while that in the *ocellaris* chromosome is commonly made up of large, block-like granules. The latter are evidently due to the presence of large droplets of achromatic material. In spite of the variations in structural details observed in each species at this "locus" it seems probable that the difference is real, for it is maintained in the hybrid where the two chromosomes are present in a single nucleus and hence are subject to the same influences. Unfortunately, it is not certain that the number of individual disks is exactly the same at this "locus" in the two chromosomes; but the evidence nevertheless suggests strongly that the difference in question is qualitative in nature and has arisen through the occurrence of one or more qualitative changes during

the differentiation of the two species from a common ancestor. (See Metz (1938*b*) and Metz and Lawrence (1938) for description of this case, with illustrations.)

There are other cases in these hybrids which may be analogous to that just discussed, but they have not yet been studied in sufficient detail to include here. It seems possible, likewise, that the small regions described by Horton (1939) in hybrids between *Drosophila melanogaster* and *D. simulans*, where the pattern is similar but synapsis is often prevented, may represent qualitative differences.

Artificial induction of chromosome rearrangements in *Sciara*

The main facts concerning this topic have been discussed previously (Metz and Boche, 1939) and will only be summarized here. (1) It has been found very difficult to induce mutation in *Sciara* by irradiating adult females. (2) Using the salivary gland chromosome technique, following a dose of 5000 r. units applied to adult flies, chromosome rearrangements (inversions and translocations) were secured with a frequency of approximately 27 % from treated males, but none was secured from treated virgin females (except in one doubtful case). In *Sciara* the eggs all mature at once, and those treated were nearly mature. It appears, therefore, that, as regards rearrangements, the chromosomes of eggs are much more resistant to irradiation at this stage than are those of sperms.

In this connexion it should be noted, through the kindness of Dr H. B. Glass, that in genetic tests for induced translocations in *Drosophila melanogaster* (unpublished), Glass was unable to secure any translocations from eggs laid within the first five days following treatment of virgin females. (This work was unknown to us until after our results were in the Press.) These findings suggest that in *Drosophila*, as in *Sciara*, mature or nearly mature oocytes are resistant to induction of rearrangements by irradiation, and hence that the phenomenon is not due to any peculiarity of *Sciara* chromosomes.

Preliminary evidence of Dr Boche and the writer tends to indicate that in the *Sciara* eggs, at the time of treatment, the chromosome pairs are well separated from one another, are in a relatively condensed (prophase?) condition, and are embedded in a relatively firm mass of nucleoplasm. It is assumed that in the sperms the chromosomes are packed relatively tightly together and are probably in a thread-like condition.

Discussion

As indicated in the foregoing account, there seems clearly to be a noticeable difference between the types of spontaneous chromosome rearrangement detected most frequently in *Drosophila* and those found most frequently in *Sciara*. The question arises, therefore, as to the evolutionary significance of the respective types of modification, and as to the nature of the mechanisms responsible for the changes.

Other workers (e.g. Dobzhansky, 1937) have shown that inversions and translocations, such as those found in *Drosophila*, provide a theoretically adequate means of bringing about evolutionary changes. Is this, then, the method by which evolutionary changes are effected in organisms generally? If it is, evolution should be progressing relatively slowly in *Sciara* as compared with *Drosophila*. It seems more probable that in *Sciara* the minute deficiencies and duplications provide a basis for evolutionary change, and that their frequency compensates for the rarity of inversions and translocations.

Such considerations, in turn, raise the question as to whether the two types of change (the *Drosophila* type and the *Sciara* type) might eventually lead to broadly different evolutionary trends. This, of course, is a question for the future, and need only be mentioned here.

Of more immediate interest is the question as to how the different kinds of change are brought about, and why there is such a difference between the two genera. It seems evident that in *Drosophila* some condition favours the production of inversions and translocations rather than minute deficiencies and duplications while in *Sciara* the situation is reversed. It should be observed that some of the minute "deficiencies" in *Sciara* may be due to the occurrence of minute translocations, as Muller (1935) has suggested in the case of *Drosophila*. But it seems improbable that this process occurs frequently here, because of the rarity of large translocations. It seems more reasonable to assume that most of the minute "deficiencies" have arisen in the same manner as the minute "duplications". Because of their nature, the latter seem best accounted for on the assumption of unequal crossing-over, a process which could also readily give the minute deficiencies. Such interpretations, however, throw little light on the physical characteristics of the chromosomes which presumably determine the nature of the modifications; and they do not indicate why conditions should differ in the two genera. These are unsolved problems. No attempt will be made here to discuss the various hypotheses which might be suggested to cover them; but, in conclusion, a few words may be said as to how they are being attacked.

In attempting to solve these problems, attention naturally falls on the fact that the rarity of spontaneous inversions and translocations in *Sciara* as compared with *Drosophila* is paralleled by the rarity of induced inversions and translocations in females as compared with males in *Sciara*. It seems possible, therefore, that by cytological comparison of the

chromosomes in eggs, where induced rearrangements do not occur, with those in sperms, where induced rearrangements do occur, we may be able to reveal at least some of the factors which are involved in the production of these rearrangements. Such a study is under way, but, unfortunately, it could not be finished in time to be reported here. The preliminary observations noted above, however, give a suggestion as to the nature of the evidence. It seems probable from these observations that the degree of attenuation of the chromosomes, the spatial relations of the chromosomes, and the viscosity of the material immediately surrounding them, will prove to be the main factors involved in such rearrangements. As regards the minute modifications found in *Sciara*, the situation may be different, but if these arise mainly through unequal crossing-over, as seems probable, the study just mentioned may also throw light on the factors favouring or interfering with this process.

In connexion with these investigations attention is, of course, being given to the relation between induced mutation and chromosome rearrangement, following the lines suggested by the results noted above. By comparing the rate of induced mutation in eggs, which do not give chromosome rearrangements, with that in sperms, which do give rearrangements, it should be possible to throw additional light on this subject.

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MICHAELIS, P. *Plasmavererbung und Entwicklungsphysiologie*

Grundlage für eine erfolgversprechende Betrachtung der Plasmavererbung muss das entwicklungsphysiologische Verhalten des Zellplasmas sein. Leider ist sein Verhalten bei der Befruchtung, bei Zell- und Kernteilung noch viel zu wenig bekannt. Von ihm ist das Sichtbarwerden der plasmatischen Vererbung, die Konstanz und Variabilität des Plasmons abhängig. Eine plasmatische Vererbung kann nur dann sichtbar und beweisbar werden, wenn das Plasma ausschliesslich von der Mutter geliefert wird. Es können dann reciprok verschiedene Bastarde entstehen. Bei einigen solchen reciprok verschiedenen Bastarden konnte eine plasmatische Vererbung eindeutig bewiesen werden, und ihr Einfluss auf die verschiedensten Vererbungsvorgänge, wie Mutationsrate, Austausch, auf Sterilität und Letalität belegt werden.

Unterschiede im plasmatischen Erbgut sind nicht für Arten und Gattungen, sondern für kleinste systematische Einheiten kennzeichnend und sie beeinflussen weniger die systematischen Merkmale, sondern sie greifen in lebenswichtige, physiologische Prozesse ein, die grossen Verwandtschaftskreisen eigen sind. Ein Beispiel ist die Veränderung des Auxin-Stoffwechsels, wahrscheinlich durch eine oxydative Zerstörung des Auxins, was zu starken Störungen des Längenwachstums führt. Weiterhin kann der ganze Kohlehydratstoffwechsel abgeändert werden. Morphologisch äussert sich das in Blattfleckung, abnormen Chloroplasten-Grössen und abweichendem Chlorophyllgehalt. Durch Änderung der Plasmapermeabilität wird der osmotische Wert, Nährstoffaufnahme und Wanderung beeinflusst. Weiterhin

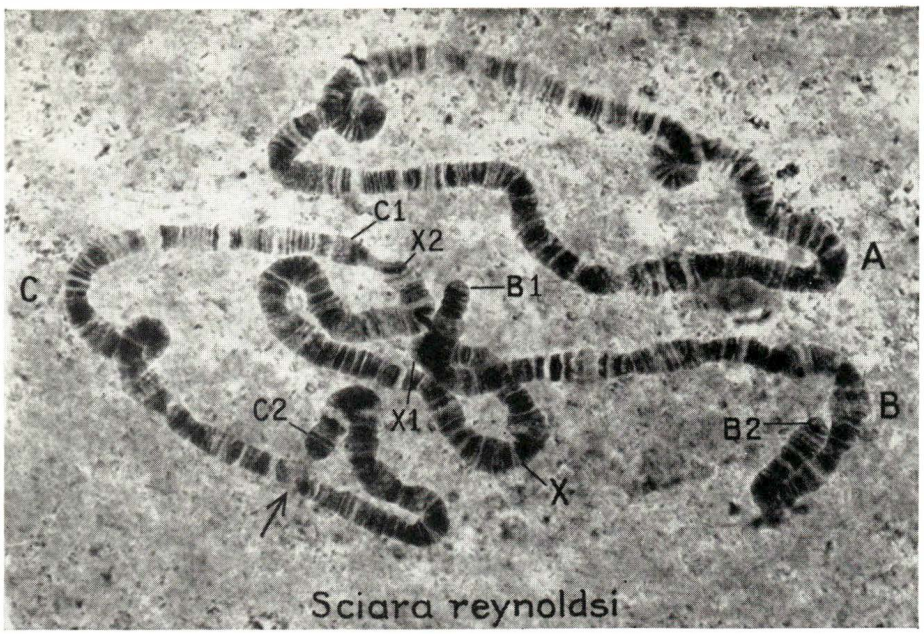


Fig. 1. Salivary gland chromosome group of *Sciara reynoldsi* Metz, from aceto-carmine smear. (Compare with the corresponding group of *S. ocellaris* Comst., in frontispiece, Metz, 1935.) The four chromosomes (pairs) are indicated by letters, *A*, *B*, *C* and *X*, and the ends of the chromosomes by numbers, 1, 2. Note the tendency of the ends to stick together or to the side of a chromosome (see arrow). Note the "figure 8" shape of the *X*-chromosome. Photomicrograph, × 500.

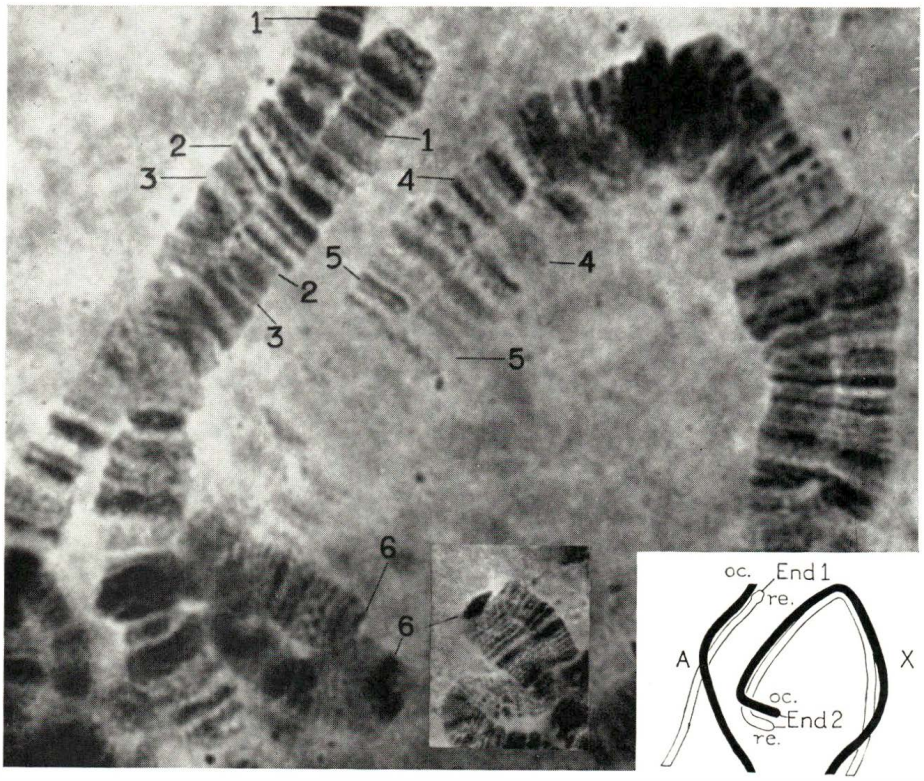
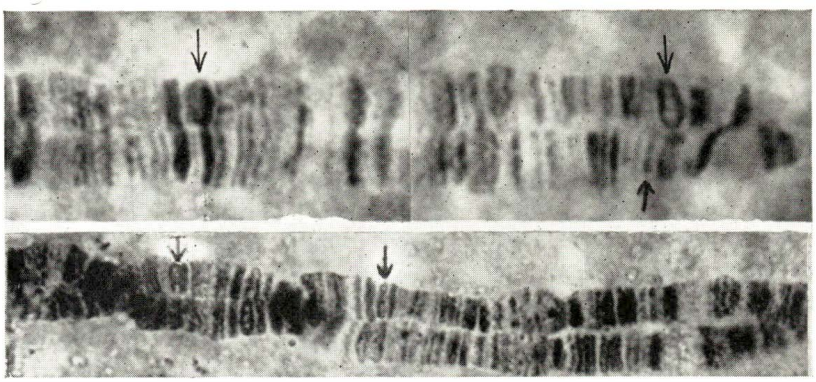


PLATE II. Fig. 2. Salivary gland chromosomes of hybrid between *S. ocellaris* and *S. reynoldsi*, showing portions of pairs *A* and *X*, as indicated in the diagram. Numbers 1–1, 2–2, etc., indicate corresponding loci where minute "deficiencies" or "duplications" appear. Conditions at 3 and 4 are uncertain, but 1, 2 and 6 are well known, and case 5 seems obvious. The inserted photograph shows the large deficiency (6) at the apex of the *X* from another preparation and at lower magnification (× 850). Photomicrograph from aceto-carmine preparation approximately × 2000.



Figs. 3, 4. Portions of salivary gland chromosomes from hybrids between *S. ocellaris* and *S. reynoldsi*, from acetocarmine preparations. Fig. 3 (above) from chromosome *A*, showing two asymmetries of the "duplication" type, indicated by upper arrows. The lower arrow at the right indicates locus corresponding to upper arrow. Photomicrograph, ×1700. Fig. 4 (below) portion of chromosome *B*, showing at the left arrow another minute "duplication" and at the right arrow a case which may be interpreted as either a duplication or deficiency. Photomicrograph, ×1133.

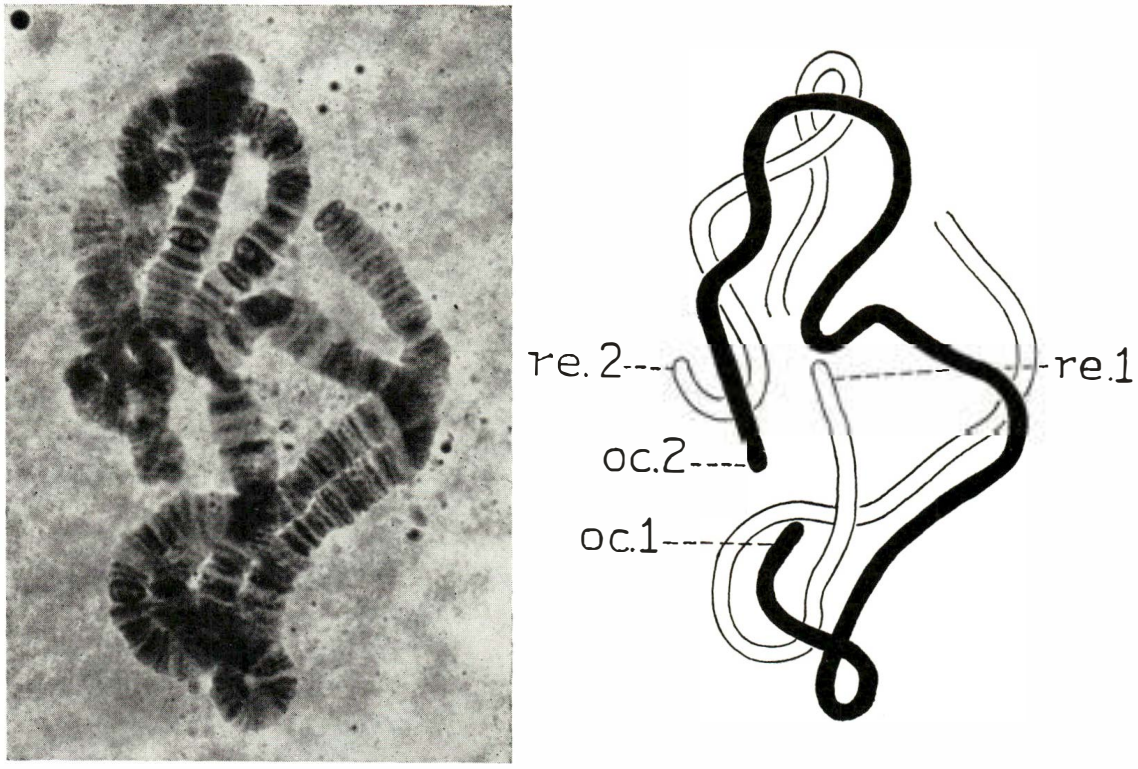


Fig. 5. Chromosome pair *C* from the hybrid, showing the *reynoldsi C* characteristically broken into two segments, which associate with the corresponding parts of the *ocellaris C*, as indicated in the diagram and described in the text. End 1 of the *reynoldsi C* is stuck to the side of the *ocellaris C*, but is not connected with the other segment from *reynoldsi*. Photomicrograph, from aceto-carmine preparation, ×700.

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können Viskosität des Plasmas und seine Resistenz abgeändert werden.

In diesen Beispielen müssen die durch Plasmonverschiedenheiten hervorgerufenen Abänderungen der physiologischen Prozesse keineswegs nur zu Störungen führen, sie können auch Ursache einer Leistungssteigerung sein. Allerdings sind entwicklungsphysiologische Störungen, die Pollensterilität (Gynodiöcisten) und Letalität verursachen häufiger und auffälliger.

Wenn die erwähnten Versuche auch methodisch so ausgeführt wurden, dass bei konstantem Genom nur die Unterschiede des Plasmons geprüft wurden, so darf das nicht zu der Meinung führen, als würde das beobachtete Ergebnis ausschliesslich auf Plasmawirkung beruhen. Die Änderung des Kohlehydrat- oder des Auxinstoffwechsels beruht auf den abgeänderten Wechselbeziehungen zwischen Plasmon und einer Anzahl, ganz bestimmter, frei kombinierbarer Gene. Bei einzelnen dieser Gene wirkt sich eine Plasma-Abänderung schon im heterozygoten, bei anderen erst im homozygoten Zustande aus. Damit wird das Problem der entwicklungsphysiologischen Bedeutung des Plasmons gleichzeitig zu einem Problem der Genmanifestation.

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MICZYŃSKI, K. ***The Inheritance of Some Characters in the Intervarietal Crosses of*** **Aegilops**

The present paper gives an analysis of some intervarietal crosses made within two *Aegilops* species, viz. *Ae. ventricosa* and *Ae. triuncialis*. The following characters were investigated: glume colour, pubescence of the glumes, waxy bloom on the ears and stems, and awnedness of the lateral spikelets.

Glume colour. Among the varieties of *Ae. ventricosa* there were found three types of the glume coloration: white, red and black. The crossing: red × black gave a black-chaffed F_1 generation, F_2 segregated into 249 black and 71 red individuals (3:1).

Waxy bloom and pubescence of the glumes. The author has isolated several strains of *Ae. triuncialis* differing in the pubescence or glabrousness of the glume surface, as well as in the presence or absence of the waxy covering on ears and stems.

The crosses waxy × waxless gave always waxless F_1 generation, the waxy condition being recessive. One part of the crosses segregated in F_2 in a ratio of 3 waxless: 1 waxy, the other crosses according to the 15:1 ratio waxless to waxy. Thus the waxless condition is dependent upon one or two dominant genes.

The crosses between the pubescent and "glabrous" types showed the dominance of the pubescent glume surface. In F_2 a segregation into pubescent and "glabrous" individuals was obtained in a ratio very close to 3:1 or 1:2:1. Two crosses showed linkage of the pubescence of the glume with the absence of the waxy bloom. This linkage, however, was not absolute, and a small number of individuals with recombined characters appeared. In one cross no linkage was observed.

The results of these crossing experiments may be explained as follows: The pubescence of the glumes is dependent upon a single dominant factor—**H**. The development of the waxy bloom is checked by one or two dominant inhibitory genes, **Z** and **Z′**. One of these genes (**Z′**) is linked with the **H**-gene for pubescence, the other (**Z**) is inherited independently. The observed numbers of the F_2 individuals were too small for the exact determination of the cross-over percentage between **Z′** and **H**. Probably it lies between 4 and 6 %.

Awnedness of the lateral spikelets. There were isolated several strains of *Ae. triuncialis* characterized by different mean length of the lateral glume awns. The crosses awnless × fully awned, awnless × awnleted, short awned × fully awned, showed in F_2 in the majority of cases a distinct preponderancy of the shorter awned parent. The detailed genetical analysis could not be done without examination of the F_3 generation. Probably a number of cumulative genes is involved.

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MIEGE, E. ***L'hérédité de la composition chimique chez les hybrides intergénériques***

ÉTUDE DE LA DESCENDANCE D'*AEGILOPS OVATA* L. VAR. *NIGRA* × *TRITICUM VULGARE* ET D'*AEGILOPS OVATA* × *TRITICUM DURUM* DESF.

Si la ségrégation morphologique, anatomique, cytologique des hybrides obéit à des règles (Naudin-Mendel) aujourd'hui bien définies, l'hérédité de leur composition chimique est beaucoup moins bien connue et, à part les travaux de H. Colin, Leveque de Vilmorin, Bouzy, Sosa-Bourdouil, Miege, n'a pas donné lieu à de très nombreuses recherches.

Nous l'avons étudiée dans la descendance des croisements interspécifiques de *Triticum* et dans ceux d'*Aegilops* × *Triticum* notamment sur les générations successives (jusqu'à la F_5) des hybrides intergénériques = *Aegilops ovata* L. var. *nigra* × *Triticum vulgare* H. var. *alborubrum* (No. 422) et × *T. durum* Desf. var. *melanopus* (No. 250). Nous résumons brièvement, ci-dessous, nos principales observations.

L'examen morphologique et anatomique a montré:

le caractère intermédiaire de la F_1, le retour partiel aux parents à partir de la F_3, la stérilité à peu près totale des lignées se rapprochant du type sauvage et la fertilité croissante des formes *Triticum*, la juxtaposition des caractères chez les individus intermédiaires. Du point de vue cytologique, la F_1 présente de nombreux monovalents qui disparaissent progressivement, tandis que les bivalents, en quantité d'abord irrégulière, atteignent peu à peu la formule chromosomique des géniteurs.

En ce qui concerne la composition chimique, il ressort des analyses que nous avons effectuées (humidité, matières, minérales, sucres, amidon, matières grasses, azote, phosphore) que:

(1) Les genres *Aegilops* et *Triticum*, malgré leurs affinités botaniques, sont nettement séparés par la composition chimique de leurs fruits.

(2) La F_1 est intermédiaire par l'ensemble de ses caractères.

(3) Dès la F_2, mais surtout à partir de la F_3, la ségrégation donne naissance à des formes faisant progressivement retour aux deux parents, et à des lignées conservant leur aspect intermédiaire.

(4) La stérilité est fréquente, et parfois totale, dans les générations successives des souches à caractères *Aegilops*; encore présente, mais beaucoup plus rare chez les individus ressemblant de plus en plus à *Triticum*.

(5) Le géniteur femelle *Aegilops* montre (pour tous les caractères considérés) une influence prépondérante, qui va, toutefois, en s'atténuant au fur et à mesure que la disjonction s'accentue—bien que la stérilité persistante des individus aegilopoiformes n'ait pas permis matières minérales, en gluten et en azote se rapproche l'analyse chimique de leurs fruits. La teneur en bien davantage de celle du parent sauvage que du blé cultivé. Il existe des cas très nets de transgression, notamment en ce qui concerne les matières amylacées et les propriétés plastiques des pâtes.

(6) Les variations du phosphore sont parallèles à celles de l'azote.

(7) Le comportement de la descendance est quelque peu différent selon que le parent mâle appartient à *Triticum durum* ou à *T. vulgare*, les hybrides de ce dernier se rapprochant plus vite, que ceux du *T. durum*, de la composition paternelle.

(8) L'ensemble de ces faits confirme les observations antérieures.

(9) Il indique, dans ces hybrides intergénériques—avec la dominance du géniteur ancestral—un retour au moins partiel et progressif vers les parents, et des caractères qui semblent autoriser à les considérer comme un exemple d'hérédité naudinienne.

(10) L'hérédité de la composition chimique paraît obéir aux mêmes règles.

MONTALENTI, G. ***Ricerche quantitative sull' azione dei geni della striatura (barring) nelle penne maschili e femminili dei polli Barred Plymouth Rocks***

Le penne dei Barred Plymouth Rocks presentano un dimorfismo sessuale nel disegno oltre che nella forma: le penne del gallo hanno colorazione più chiara di quelle della gallina, e ciò dipende dalla maggiore ampiezza delle strisce bianche rispetto alle nere. La striatura è un carattere legato al sesso, determinato cioè da geni localizzati nei cromosomi *X*. Perciò tale differenza è generalmente considerata come dipendente dal fatto che il maschio è omozigote per il fattore striatura, e poichè questo determina la comparsa delle strisce bianche in una penna di colore uniforme, si ammette che una doppia dose del gene della striatura (*B*) determini una maggiore ampiezza della striscia bianca.

In collaborazione con la Dott. A. Agostini, ho esaminato quantitativamente tale dimorfismo sessuale del disegno delle penne, con l' intento di studiare l' azione di diverse dosi dei geni *B*. Questo dimorfismo non è sotto il controllo degli ormoni sessuali, perchè si trova anche nel piumaggio giovanile, e non è alterato dalla gonadectomia nè dall' iniezione di ormoni del sesso opposto, come è dimostrato dagli esperimenti e dalle misure all' uopo eseguite. E' dunque determinato dalla costituzione genetica, probabilmente per azione diretta dei geni durante la formazione delle penne, come starebbe ad indicare il fatto, dimostrato da C. H. Danforth, che il trapianto di pelle su polli di razza diversa non altera il disegno tipico delle penne del donatore Barred Plymouth Rock.

E' stata misurata l' ampiezza di una doppia striscia (nero + bianco) e della striscia nera (sempre nella terza doppia striscia a partire dall' apice della penna) in penne omologhe del maschio e della femmina, in cui non vi è dimorfismo di forma (penne dell' alto petto). L' ampiezza della doppia striscia della penna femminile è *circa* 1·3 volte quella della penna maschile. La striscia nera è nella penna femminile *circa* 2/3 della doppia striscia, nella penna maschile *circa* 1/2.

Pertanto la doppia dose del gene striatura (*barring*) nel maschio produce: (*a*) un ritmo più accelerato nella formazione del disegno, perchè la doppia striscia è del 30 % *circa* più bassa che nella femmina; (*b*) un' ampiezza della striscia bianca che risulta pari a quella della femmina moltiplicata per 1·5 *circa*. Perciò le azioni dei geni della striatura, in quanto determinanti la formazione della striscia bianca, non si sommano semplicemente. La espressività (nel

senso di Timoféeff-Ressovsky) di *BB* non è eguale al doppio della espressività di *B*.

Simili relazioni valgono anche per il piumaggio giovanile.

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MULLER, H.J. ***The Mechanism of Structural Change in Chromosomes***

Genetic tests of the past year (Muller, Sidky, Makki *et al.*) fully confirm the earlier results of Muller, Belgovsky and other collaborators that the frequency of all gross structural changes that survive varies as the 3/2 of the dose of radiation applied to *Drosophila* spermatozoa, for the range from 1000 to 4000 r. This applies not only to ordinary translocations but also to those involving the "cubitus" effect and to gross deletions (contrary to conclusions by Dubinin's collaborators). That this relationship cannot be explained on the "contact" hypothesis, as an indirect, combinational effect of the ionizations, is shown by further experiments of the past year (Muller, Raychaudhuri and Makhijani), proving that, for a given *final* (total) dose, the frequency of these changes remains constant, regardless (*a*) of wave-length, for the range between γ and 50 kV. X-rays; (*b*) of continuousness of application of dose or its fractionation over a three-week period; (*c*) of immediate or one-month-postponed fertilization by the treated sperm; (*d*) of radiation intensity, for the range from 0·01 to 200 r. per min.; (*e*) of temperature during treatment, from 4 to 36° C. Tables are presented giving the summarized data for each of these series of experiments.

These findings prove that there are primary effects (presumably breakages) produced individually by the ionizations acting independently of one another, without regard to their time and space distribution (within the above limits), just as gene mutations are produced, and that these primary effects are stored up throughout the duration of the spermatozoon stage, i.e. until fertilization, when they must interact with one another to give the final structural changes (rearrangements) as secondary effects, that represent combinations of two (and often more) of the primary changes.

If these primary effects are really breakages, those fragments which failed to reunite in due time would result in losses of the affected chromosome (since, being without telomeres, their chromatids would eventually unite to form dicentric and acentric chromosomes as McClintock has shown), and the frequency of these losses, referable to individual primary breakages ("single breaks"), should then vary approximately linearly with the dose. Recent experiments (Muller, Singh *et al.*) give evidence of such a relation for whole-chromosome losses, unlike that for two-break or multiple-break rearrangements, and thus confirm the "breakage first" hypothesis from another angle; the results, however, show that only a small proportion of broken ends thus fail to rejoin in due time. Work is in progress (Pontecorvo and Muller) to obtain further evidence that the losses in question result from "simple breaks".

The fact that the exponent (3/2) is lower than the square does not indicate that some of the rearrangements result from two or more breaks produced by single ionizations (as on a form of the contact hypothesis), for calculations (of Pontecorvo and Muller, following Haldane, Stadler, and Catcheside) show that the increased proportion of inviable combinations formed with high doses, as a result of multiple independent breaks, is adequate to account for the observed deviation from the square relation in our experiments. (In Sax's experiments the deviation from the square was not so caused, since inviability did not enter in, but was caused by (1) the inclusion of simple breakage cases, in which union had not yet occurred, and (2) the fact that recombination could occur during treatment, leading to a dependence of some of the results on the time-intensity relation.) Further calculation shows that the observed exponent would rise, approaching nearer to the square, at a lower range of dosages, if all recombinations result from independent breaks, whereas if some are due to two or more breaks produced by single ionizations, rearrangements so produced would tend to predominate at lower doses, so that in this case the exponent would fall at lower doses, approaching nearer to *l* (linearity). Our results indicate that the exponent does not fall at lower doses (400–1500 r.), but probably rises, as expected for breaks all of which are independently produced. The existence of triple and still more multiple-exchange rearrangements (Muller, 1934, 1935; Dubinin and Khvostova, 1935) likewise favours this conclusion. So also does the finding of a translocation between paternal and maternal chromosomes (Sidky).

Multiple break translocations involving transference ("deletion insertion") of an interstitial section were sifted out from the rest by tests with a ring chromosome, as compared with non-rings. Results (Muller and Sidky) show such multiple-break cases to be more frequent, relative to double-break cases, than chance breakage and recombination of broken ends would allow. Unless there is a considerable proportion of minute transfers here (see below), it can be concluded from this that initial proximity of broken ends favours their reunion; and from this in turn that restitutions must be the most probable combinations.

Whereas virtually all gross structural changes in-

duced by radiation thus result from independent breaks produced by two or more separate ionizations, experiments of Muller and Makki confirm and extend the earlier evidence (Belgovsky) that induced minute rearrangements result from breaks dependent on one and the same ionization, the effect of which spreads to neighbouring points on the coiled chromosome. This applies both to minute rearrangements in and near heterochromatic regions, which are especially prone to breakage (including this multiple breakage), and to those in other regions, as shown by the linear relationship, like that for "gene mutations", between their frequency (of yellow in scute-8, of Notch, etc.) and the dose. It is not yet known whether or not one ionization can break two nearby (sister) chromatids in *Drosophila* (as described by Sax for *Tradescantia*); but tests of Offermann (unpublished) on ring chromosomes show that lethals can seldom be caused by attachment between sister rings broken at nearby points.

The frequencies of induced genetic changes of various types—gene mutations, minute rearrangements, and gross structural changes—is calculated to be high enough to explain the order of magnitude of the mortality of zygotes derived from eggs fertilized by irradiated spermatozoa. Their death then must be, largely at any rate, of genetic origin; at high doses the gross rearrangements tend to be the preponderant cause of these deaths. On the other hand, the mortality of zygotes from irradiated eggs and early developmental stages must be largely non-genetic ("physiological"), as shown by the small amount of genetic change induced by highly lethal doses and by the similar resistance of triploids and diploids (Muller and Lamy, this congress). In which class the necrosis produced in rapidly growing tissues of adults belongs, remains to be determined. In so far as structural change contributes to this necrosis, the latter would be dependent on radiation intensity and other conditions accompanying treatment, since combination of broken ends could occur in such cells during treatment, and on the cell stage irradiated, since this would influence likelihood of restitutional as opposed to other combinations, and perhaps also likelihood of breakage.

Identity of frequency-dosage relations of induced minute rearrangements and gene mutations makes more acute the question (Muller, Goldschmidt) of whether there is any distinction between them except one of degree. That the minute rearrangements induced by high-energy radiation involve actual chromosome breakages, occurring before reunion and resembling those of gross rearrangements, is indicated by the former sometimes being combined with the latter (as in scute 19 and in Oliver's facet-locus deletion insertion), though quantitative data on this question are still needed. But the gene mutations induced by ultra-violet do not involve preliminary breakages of the chromosomes, at least, not thoroughgoing breakages like those produced by X-rays, for if they did gross rearrangements would be produced in abundance by ultra-violet, and they are not so produced (Stadler and Uber, 1938, in maize; Muller and Mackenzie, 1939, in *Drosophila*). (The terminal deficiencies produced in maize by ultra-violet may therefore be due to gene mutations which result in unipolar genes—telomeres—thus secondarily breaking the chromosomes and making one fragment at least non-combinable.) This gives ground for supposing that the gene mutations may be different, structurally, from minute rearrangements, but the question is far from settled. Data now being sought on whether ultra-violet and other agents of relatively low energy concentration produce minute rearrangements should have a bearing on the problem.

If the gene mutations are only ultra-minute linear rearrangements we should have to suppose that breaks can be "intragenic", and in so doing we should in part remove the supposed boundaries between genes (see Muller, 1926). In this case some "gene mutations" produced by ultra-violet should straddle supposedly different genes (even such as did not have direct position effects on one another). Speaking for such boundaries, however, are (1) the observations on the number of genetically detectable breakage points in limited regions (Muller and Prokofyeva, 1934—although these might be explained away by postulating relatively long stretches of genetic material of low phenotypic activity lying between the critical "genes"); (2) considerations regarding the mechanism of precisely "equal" crossing-over; and (3) the fact that broken ends are not of alternative signs, as they would be if broken between amino-acid connexions.

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MÜLLER, K.O. ***Physiologisch-genetische Untersuchungen zur Analyse der*** **Phytophthora-*Resistenz der Kartoffel***

Nach Auffindung von südamerikanischen Primitivkartoffeln, die sich durch eine hohe Resistenz gegenüber der *Phytophthora infestans* auszeichnen, und durch Kreuzung dieser Formen mit unseren anfälligen europäischen Kulturkartoffeln sind im Laufe der letzten 15 Jahre an der Biologischen Reichsanstalt jene Neuzuchten entstanden, welche die wertvollen Eigenschaften der letzteren mit der Resistenz gegenüber der Biotypengruppe A des Parasiten verbinden. Der Unterschied zwischen den resistenten "*W*-Sorten" und den anfälligen Kultursorten im Verhalten gegen-

über dem Parasiten ist genotypisch bedingt. Wie vor mehr als neun Jahren bereits dargelegt, lässt sich die Verteilung der "Resistenzgene" auf die Nachkommen am zwanglosesten auf dem Grunde der Theorie von der tetraploiden Struktur der europäischen Kulturkartoffel erklären.

Im Anschluss an diese Ergebnisse gilt es, die Wirkungsweise dieser Resistenzgene zu analysieren. In erster Reihe war zu klären, ob sie bei der Pflanze *a priori* einen "Zustand" bedingen, der eine gedeihliche Entwicklung des Parasiten ausschliesst, *oder* ob erst die *Reaktion* der mit den Parasiten in Kontakt gelangten Wirtszelle die Hemmung der Pilzentwicklung auslöst. Auf experimentellem Wege wurde der Nachweis erbracht, dass die zweite Alternative zutrifft: Die von dem Parasiten erfassten Wirtszellen erleiden charakteristische Veränderungen, die schliesslich in den Todzustand einmünden. Bevor dieser erreicht wird, kommt es jedoch zur *Entstehung* eines für den Parasiten toxischen Prinzips. Dieses ist stofflicher Natur. Alles deutet darauf hin, dass das wirksame Prinzip zur Gruppe der Gerbstoffe gehört, wie schon vor uns Dufrénoy angenommen hat.

Seine Wirkung ist unspezifisch. D.h. es wirkt nicht nur auf *Phytophthora infestans*, sondern auch auf andere Mikroben entwicklungshemmend.

Zu dieser "Abwehrnekrose" sind, was zunächst überrascht, nicht nur die Resistenten, sondern auch die Anfälligen befähigt. Denn der Endzustand, den die Zellen erreichen, nachdem sie mit dem Parasiten in Kontakt gelangt sind, ist in beiden Fällen der gleiche. Nur darin unterscheiden sich, wie die vergleichenden entwicklungsgeschichtlichen und zellphysiologischen Untersuchungen lehrten, die anfälligen von den resistenten Genotypen, dass sie dasjenige Stadium der Nekrobiose, bei der jene "Antistoffe" wirksam werden, viel zu spät erreichen, als dass der Parasit in seiner Entwicklung noch irgendwie gehemmt werden würde.

Hiernach bestehen also zwischen den Anfälligen und Resistenten keine "prinzipiellen", sondern nur "graduelle" Unterschiede, was auch auf einem anderen Wege bewiesen werden konnte: Lässt man nämlich auf infizierte Knollen von anfälligen Sorten niedrige Temperaturen einwirken (3–6° C.), bei denen die Entwicklung des Parasiten nur noch sehr langsam, die Abwehrnekrose dagegen immer noch relativ schnell verläuft, so verhalten sich die Anfälligen ebenso wie die Resistenten. Entscheidend ist also für das Endergebnis das Verhältnis zwischen der Entwicklungsgeschwindigkeit des Parasiten und der Reaktionsgeschwindigkeit der Wirtszelle.

Diese Erkenntnisse lassen die Wirkung der "Resistenzgene", durch die sich die *W*-Sorten von den anfälligen Kultursorten unterscheiden, in einem ganz neuen Licht erscheinen. *Die massgebenden Gene bedingen keine "Alles- oder Nichts"-Reaktion, sondern fungieren lediglich als "Accelatoren", indem sie den Ablauf einer Reaktion beschleunigen, zu der ebenso wie die resistenten auch die anfälligen Genotypen befähigt sind.* Hiermit ist die Frage müssig geworden, ob die *Phytophthora*-Resistenz als erworbene *oder* angeborene Immunität zu gelten hat. Betrachtet man die Dinge vom rein phänomenologischen Standpunkt, so handelt es sich um die Form der erworbenen Resistenz; denn der "resistente Zustand" wird ja erst verwirklicht, *nachdem* die Zelle mit den Parasiten in Kontakt gelangt ist. Tritt man dagegen von der genetischen Seite an das Problem heran, so sind eigentlich die "Gene" die ausschlaggebenden Faktoren; denn sie entscheiden ja über die Geschwindigkeit, mit der die Abwehrnekrose zum Ablauf gelangt. Es besteht also im Grunde genommen zwischen den beiden Ansichten keine Gegensätzlichkeit; nur der Standpunkt, von dem aus die Dinge betrachtet werden, ist verschieden.

Die Untersuchungen wurden von dem Vortragenden gemeinsam mit seinen Mitarbeitern H. Börger, M. Klinkowski und G. Meyer durchgeführt.

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Munro, T.A. *The Genetics of Phenylketonuria*

In 1934, Folling described ten mentally defective patients who excreted phenylpyruvic acid in the urine. This inborn error of protein metabolism, always associated with mental defect, had not been found before in man. In one case, Penrose found multiple tumours on the peripheral nerves similar to those found in some types of neurofibromatosis. We suggest the phenylketonuria.

Phenylpyruvic acid is easily identified in urine by the appearance of a green colour on adding ferric chloride. Penrose showed that the disease was probably inherited as a recessive character. Jervis, in America, has confirmed this. Phenylketonuria is rare. I found thirty cases among 2411 imbeciles and idiots in institutions in Britain. The incidence of the disease in the general population is about 0·002 %.

This paper consists of an analysis of forty-three families containing forty-seven sibships in which there were seventy-three undoubted cases of phenylketonuria, and a further twelve probable cases. The disease shows marked segregation in the sibships as regards both the mental defect and the biochemical abnormality. The urines of fifty-four healthy normal sibs who could be examined contained no phenylpyruvic acid. None of the ninety-four parents was mentally defective, and the urine of forty-five parents tested contained no phenylpyruvic acid. Five of the forty-seven parental marriages were consanguineous.

The high rate of parental consanguinity, the absence of the disease in the parents and its familial incidence and segregation in the sibs prove recessive inheritance. The incidence of phenylketonuria in the sibships according to Weinberg's brother and sister method is 25·7 % ± 2·9. Using Hogben's method of factorial analysis, the difference between the observed number of sibs affected and the number expected to be affected on the hypothesis of determination by a single recessive gene is 7·6 with a standard error of ± 5·4.

The incidence of phenylketonuria among other relatives is nil in twenty-three half-sibs, nil in sixty-two grandparents, two cases in 416 uncles and aunts and two cases in 571 first cousins.

The sex ratio in the sibships is, males, twenty-one affected out of 106; females, forty-seven affected out of 120. There is no clinical evidence that phenylketonurics of one sex are more severely affected than those of the other. No phenylketonuric had married or had borne children. Although some idiots died in infancy and were probably phenylketonuric, the deaths under five years of age do not exceed expectation. There is no evidence of partial sex linkage.

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MUNRO, T.A., PENROSE, L.S. and TAYLOR, G.L. ***A Study of the Linkage Relationship between the Genes for Phenylketonuria and the ABR Allelomorphs in Man***

The paper describes the analysis of twenty-five sibships in search of genetic linkage between the gene for phenylketonuria and the *ABR* allelomorph series. The sib-pair method gives results which suggest that the loci of the two sets of genes are situated on the same chromosome. The application of *u*-function technique presents some difficulties because not all the parental genotypes could be identified. If the value of the *u*-function for each sibship is weighted in accordance with the probability that the sibship gives information about linkage, a significantly positive result is obtained.

210

MÜNTZING, A. ***Incompatibility and Fertility in Experimental and Natural Polyploids***

A typical feature of experimental autotetraploids and many amphidiploids is the occurrence of a more or less pronounced barrier of incompatibility between them and their original diploid forms. New data in this respect have been obtained in barley, rye and *Galeopsis pubescens*. A quite similar behaviour is characteristic of natural intra- and interspecific polyploids. Evidently simple quantitative conditions are of great importance for the development and preservation of the polyploid series found in nature. Due to the occurrence of incompatibility barriers, chromosome doubling may lead to quite new possibilities of hybridization. This has, for example, been found in *Galeopsis*, with respect to allo- as well as autotetraploid forms.

Fertility and cytological stability in allo- as well as autopolyploids is partly a biotype question. In barley tetraploid strains derived from different diploid biotypes were found to differ significantly as regards fertility and frequency of aberrants in each generation. In strains of *Triticale* different degrees of fertility and cytological stability were also found. Thus, it may be possible by recombination to produce quite fertile and stable *Triticale* types. Natural polyploids, as a rule, are more fertile than the polyploids experimentally induced. The recent experimental results make it possible to understand how fertility in experimental or newly arisen natural polyploids may be improved by a direct selection or by selection and recombination.

211

MURARI, T. ***Cross-breeding Experiments with Cattle in the Madras Presidency***

This paper reports work done in various cattle crosses at the research farm at Hosur. The Indian breeds involved were the Sahiwal (Montgomery), Sind, and Coimbatore. European blood is represented by the Ayrshire. Details of colour inheritance are given. The zebu hump disappears (but not completely) in the first cross with Ayrshire, but traces may be found in subsequent generations of halfbreds. Backcrossing to the zebu brings back the hump. The coat and udder are described. The F_1 by Ayrshire give more milk than their native dams and exhibit signs of heterosis. Greater care is required for the management of the F_1.

212

MURPHY, D.P. ***Reproductive Characteristics of Parents of Congenitally Malformed Children***

Study based upon information regarding 890 families, each possessing at least one child who exhibited a gross, congenital malformation at the time of birth. Families located through the medium of diagnosis upon death certificates. Survey includes all families who were living in the City of Philadelphia, who gave rise to a malformed member that died between 1 January 1929 and 31 December 1934. Information secured from the following sources: (A) Birth certi-

ficates, (B) Death certificates, (C) Interviews with 546 mothers in their homes, (D) Inspection of hospital birth and death records, (E) Consultations with family physicians. There was a total of 935 malformed offspring in the above families.

Report deals with the following characteristics:

(1) General incidence of gross, congenital malformations.

(2) Incidence of malformations in relation to race and syphilis.

(3) Maternal age and parental age difference.

(4) Reproductive rate.

(5) Place in family of miscarriages, premature births and still-births.

(6) Intervals between pregnancies.

(7) Birth order of malformed children.

(8) Duplication of malformations among siblings.

213

MURPHY, D.P. ***The Outcome of 625 Pregnancies in Women Subjected to Pelvic Radium or Röntgen Irradiation***

Study of the outcome of a series of pregnancies in 625 women who received pelvic radium or röntgen therapeutic irradiation either before or after conception. Data secured from a review of the literature and from the answers to a questionnaire sent to more than 1700 leading gynecologists and radiologists in the United States. The material concerns the effect of the irradiation upon the duration of pregnancy and upon the health and development of the subsequent children. Emphasis is laid upon the effect of post-conception therapeutic radium and röntgen irradiation on the prenatal development of the central nervous system. Several personal observations are cited.

214

NACHTSHEIM, H. ***Krampfbereitschaft und Genotypus, nach Untersuchungen am Kaninchen***

Durch Injektion von Cardiazol (Pentamethylentetrazol) lässt sich bei Mensch und Tier ein epileptischer Krampfanfall auslösen. Nach Schönmehl, Langelüddeke, Stiefler, Langsteiner u.a. antwortet ein an erblicher (genuiner) Epilepsie leidender Mensch schon auf eine geringere Dosis Cardiazol mit einem Krampf als ein von nicht-erblicher (symptomatischer) Epilepsie Befallener und als der Nicht-epileptiker. Der induzierte Cardiazolkrampf hat also hiernach differentialdiagnostischen Wert.

Mit Rücksicht auf die grosse rassenhygienische Bedeutung dieser Frage hat der Vortragende den Zusammenhang zwischen Krampfbereitschaft und Genotypus vermittels des Cardiazolkrampfes im Tierversuch geprüft, und zwar an krampfbereiten und nicht-krampfbereiten Kaninchen.

Beim Kaninchen sind epileptische Spontananfälle nur innerhalb *einer* Rasse bekannt, bei dem leuzistischen Weissen Wiener. Einzelne Familien dieser Rasse zeigen eine besondere Neigung zu Anfällen. Die Krampfneigung ist die Auswirkung eines Allels für den Leuzismus. Das Gen x ruft *nur* den Leuzismus hervor (xx = epilepsiefreier Weisser Wiener), ein zweites Allel x_e schafft *ausserdem* die erhöhte Krampfbereitschaft ($x_e x_e$ = epileptischer Weisser Wiener). x ist dominant über x_e. Zum Vergleich mit den epileptischen Weissen Wienern wurden Kaninchen fast aller anderen Rassen bzw. Genotypen benutzt.

Es wurde ausgegangen von der geringsten Dosis Cardiazol, die bei intravenöser Injektion nach früheren Untersuchungen an nicht-epileptischen Kaninchen einen generalisierten Krampf auszulösen imstande ist: je kg Körpergewicht 0·08 ccm. einer 10 prozentigen Cardiazollösung in Schüben von 0·02 ccm., alle 1½ Sekunden ein Schub. Die Ergebnisse von fast 500 Versuchen an etwa 250 Tieren sind kurz folgende.

Der Cardiazolkrampf und der Spontananfall stimmen in ihrem Ablauf überein. Eine grössere Variationsbreite des Cardiazolkrampfes wird einerseits dadurch vorgetäuscht, dass schwache Reaktionen bei Spontananfällen meist der Beobachtung entgehen, andererseits kommt sie dadurch zustande, dass bei Überdosierung, d.h. bei Überschreitung der Krampfschwellendosis, verstärkte Nachwirkungen auftreten.

Bei Jungtieren ist die Krampfbereitschaft grösser als bei Alttieren, doch reagieren in beiden Altersstufen die Epileptiker, allgemein betrachtet, auf eine weit geringere Dosis Cardiazol mit einem generalisierten Krampf als Nicht-epileptiker. Während, z.B., auf die genannte Minimaldosis Cardiazol hin unter den Alttieren 83 % der epileptischen Weissen Wiener krampften, antworteten nur 3 % der Vertreter anderer Rassen darauf mit einem kompletten Anfall.

Trotzdem ist es nicht möglich, eine Minimaldosis Cardiazol anzugeben, bei der *nur* der Epileptiker und *jeder* Epileptiker krampft, und zwar deshalb nicht, weil beim Epileptiker die Krampfbereitschaft sehr starken individuellen Schwankungen unterworfen ist. Selbst ein schwerer Epileptiker (mit häufigen Spontananfällen) kann einmal auf die obige Minimaldosis Cardiazol in keiner Weise ansprechen, ein anderes Mal, im Zustande höchster Krampfbereitschaft, schon auf die halbe Dosis mit einem generalisierten Krampf reagieren. Nicht-epileptiker verhalten sich in aufeinanderfolgenden Versuchen in der Regel ziemlich konstant.

Auch die Latenzzeit (vom Ende der Injektion bis zum Beginn des Anfalls) ist ein Ausdruck für die

Schwankung der Krampfbereitschaft beim Epileptiker. Während der Nicht-epileptiker, wenn er überhaupt reagiert, innerhalb weniger Sekunden (durchschnittlich 9) den Anfall bekommt, schwankt beim Epileptiker die Latenzzeit zwischen 0 und 90 Sekunden.

215

NEEL, J. ***Temperature, Body Size and Character Expression in*** **Drosophila**

The expression of many wild-type and mutant characteristics of *Drosophila* has been shown to vary with the temperature at which development proceeds. It has also been shown that in a number of cases there is at constant temperature a correlation between fly size and the manifestation of a characteristic. Since it is well known that under optimum feeding conditions the imaginal size of *Drosophila* varies inversely with the temperature prevailing during development, a question arises: How are size changes from one temperature to another linked with the effect of temperature upon character expression?

The following constitutes a step in the analysis of this question. A decrease in the developmental temperature to which polychaetoid *D. melanogaster* were subjected, from 29 to 14° C., resulted in an increase in the mean number of dorsocentral bristles present per side per fly (*M dc*), from $3{\cdot}058 \pm 0{\cdot}022$ to $4{\cdot}533 \pm 0{\cdot}033$. But at the same time average fly weight increased from $0{\cdot}787 \pm 0{\cdot}003$ to $1{\cdot}061 \pm 0{\cdot}006$ mg. That this weight change might be linked with the *M dc* change was suggested by the fact that when groups of polychaetoid flies are raised at varying nutritional levels at a constant temperature, *M dc* is proportional to average body size, in such a manner that a plot of log. *M dc* against log. average body weight yields a straight line.

The equations for the regression of *M dc* on body weight at 14, 19, and 24° C. were established. From these it could be shown by either of two approaches that of the total *M dc* change observed over the entire temperature range employed, the greatest part was correlated with the effect of temperature upon imaginal size. If flies were of equal sizes at all temperatures, the "temperature effect" would be greatly reduced. The relative importance of a direct effect of temperature upon the bristle-forming process (as this is contrasted with the indirect effect linked with the size factor) is greatest at a low temperature.

The partial larval starvation method used in securing groups of flies of various average sizes, for the derivation of the regression equations, results in an increase in length of larval life. It was shown that this increase had no effect upon the *M dc*.

A similar analysis has been conducted on the effect of temperature on the manifestation of the Dichaete mutant of *D. melanogaster*. Here it can be shown that when allowance is made for the size increase at the lower temperature, the "temperature effect" on the *M dc* is practically eliminated.

216

NICHOLS, J.E. ***Genotype and Environment. Some Aspects of Selection of Merino Stock for Wool Production under Pastoral Conditions***

Fleece and staple form, as well as fleece weight, can undergo marked changes in response to environment, and the type most profitable or suitable under one habitat is not necessarily so under another, even within the same breed or general type. In the pastoral areas, the metabolic potential of production, or the expression of the genetic potential, is usually less than under the more intensive conditions wherein stud breeding is practised and the parent studs tend to be aggregated.

In the Australian Merino a number of varieties have been developed in different parent studs, but certain local similarities in stud types have been manifested. Management and selection in the stud districts have led to high producing types most frequently selected for those districts and consisting of the most successful expression (in the stud master's opinion) of genetic wool characters which that environment allows. There is thus an imposed limit to which genotypic selection can be therein applied, together with another limit arising from the possibility of inadequate techniques of distinguishing between genetic variation and environmental modification.

But the great majority of commercial Merinos are depastured under conditions widely different to these favoured stud conditions; the commercial breeder is concerned with the actual production in weight and form under his own habitat, and from the genotypes available to him for importation he has to select those which apparently give a reasonably favourable response to his local environment. Classing and selection within his flock are likewise limited by the type and direction of this response, yet the trends of response in the original (stud) and in the local (commercial) environments may be antipathetic. Suitable adjustment of type to local environment may thus be handicapped genetically.

Improvements in husbandry in pastoral areas may raise production capacity and permit some degree of genetic improvement, but on the whole there are grave practical difficulties in attempting in pastoral regions to simulate features of intensive husbandry.

The pastoral conditions of commercial production being less favourable than the intensive stud conditions, the major problem appears to be to direct the trend of stud selection so that performance in pastoral environments is the objective.

This would seem to involve a certain inversion of policy on the part of many stud breeding propositions—performance in the stud locality being replaced by progeny performance tests in pastoral environments. Some studs do adopt the policy of making pastoral production the chief test, selecting for those genotypes that give the combinations of fleece and fibre characters which experience shows suitable to pastoral husbandry; in these cases the trends of both pastoral and stud selection are the same, and this principle seems to have, on genetical grounds, the greater promise of success. Another approach is through the selection of genotypes whose wool characters respond little to environmental changes; this requires much further investigation, especially in the direction of establishing criteria for the practical sheepbreeder to use.

217

OEHLKERS, F. ***Meiosis und "Crossing-over"***

Unsere Studien zur Physiologie der Meiosis sind gegenwärtig so weit gefördert worden, dass die oft erörterte Frage nach der zytologischen Basis des genetischen "crossing-over" mit neuen methodischen Mitteln angegriffen werden kann. Wir hatten ursprünglich begonnen, den Einfluss äusserer und innerer Bedingungen auf den Ablauf der Meiosis, insbesondere der Konjugationsphase, zu studieren. Als Teststadium für die Beurteilung des Einflusses solcher Bedingungen verwandten wir zunächst den jeweiligen Zustand der Diakinese, eines Stadiums, das für quantitative Beurteilungen ganz besonders günstig ist. Das erste Ziel unserer Untersuchungen bestand darin, die Eignung dieses Stadiums zu erweisen. In der Tat zeigt sich in allen Versuchen die Reproduzierbarkeit aller Einflüsse auf die Zahl der Endverbindungen in der Diakinese, sowie ihre zahlenmässige Abhängigkeit von Quantität und Qualität der angewandten Bedingungen. Der nächste Schritt bestand in dem Nachweis, dass der Zustand der Diakinese nicht allein für dieses Stadium charakteristisch ist, sondern gleichzeitig auch Auskunft über das Verhalten der Chromosomen in früheren Stadien ergibt; d.h. es musste nachgewiesen werden, dass mit einer Veränderung in dem Bindungszustand in der Diakinese auch gleichzeitig eine entsprechende Veränderung in der Chiasmenfrequenz früherer Stadien gefunden wird. Dieser Nachweis wurde von Straub an verschiedenen Objekten gebracht, insbesondere an *Campanula persicifolia*. Damit war der Zusammenhang zwischen unseren Versuchen und den neueren Vorstellungen über Bildung und Funktion der Chiasmen gegeben: die Endverbindungen der Diakinese sind ihrerseits nichts anderes als auch Chiasmen; wird durch die Einwirkung irgendwelcher Bedingungen die Anzahl der Chiasmen geändert, so muss das gleichzeitig einen Einfluss auf die Anzahl der Endchiasmen in der Diakinese haben. Kausalverbindung beider Phänomene liegt nahe; umgekehrt, die Möglichkeit einer Beurteilung früher Chiasmenbildung durch die Diakinese ist gegeben.

Dieser Befund lässt noch eine Erweiterung zu: falls die Chiasmen die zytologischen Orte des genetischen "crossing-over" sind, muss mit einer Veränderung der Chiasmenzahlen durch äussere Bedingungen gleichzeitig eine entsprechende Veränderung des "crossing-over"-Wertes unter den Nachkommen so behandelter Pflanzen herbeigeführt werden. Damit wäre der oben angedeutete "crossing-over"-Beweis geliefert. Dieser Nachweis wurde von mir selbst an *Oenothera* und von Ernst an *Antirrhinum* gebracht. Wir konnten zeigen, dass Temperaturveränderungen, die den Bindungszustand der Diakinese ändern, gleichzeitig und in demselben Sinn auf das "crossing-over" einwirken, ferner dass ebenso die Veränderungen des Wasserzustandes der Pflanzen wirken. Neuere Versuche von Ernst an *Antirrhinum* haben zeigen können, dass eine exakte Parallele zwischen Diakineseveränderungen und "crossing-over" zu finden ist und weiter wie die Temperaturwirkung überhaupt zu verstehen ist. Massgebend für die von uns beobachteten Veränderungen ist lediglich der Wechsel, nicht aber die absolute Höhe der Temperatur. Ein Übergang von der Normaltemperatur von 20° zu der tieferen von 10° führt bei *Antirrhinum* zunächst einen Abfall der Chiasmen- und "crossing-over"-Werte herbei; beide Werte steigen bei längerer Einwirkung der tiefen Temperatur wieder auf ihre normale Höhe. Denselben Einfluss ergibt der rückwärtige Übergang von 10 zu 20°, wobei nach kurzer Zeit ebenfalls wieder normale Konjugationsverhältnisse hergestellt sind.

Die hier aufgewiesenen Korrelationen bildern einmal einen wertvollen Beweis für die zytologische Basis des "crossing-over", zum anderen ermöglichen sie die Gesamtheit der äusseren und inneren Bedingungen zu bestimmen, die bei den Pflanzen einen Einfluss auf die "crossing-over"-Werte besitzen. Wir haben heute schon einen nahezu vollständigen Überblick darüber, welche Einflüsse die wirksamsten sind. Das noch vor wenigen Jahren vollkommen unangegriffene Problem des Einflusses von Aussenbedingungen auf Konjugationsphase und "crossing-over" bei den Pflanzen ist damit bereits in seinen wesentlichen Zügen umrissen.

218

Olah, L. *Interspecific Hybrids in the Genus* **Phleum**

Cytological studies were undertaken on the offspring of hybrids between *Phleum pratense* ($2n=42$) × *P. alpinum* ($2n=28$) and *P. pratense* var. *nodosum* ($2n=14$) × *P. alpinum* ($2n=28$). Amongst the offspring of the hybrids one fertile plant was obtained which had 42 chromosomes. This plant was derived from a hybrid with 21 chromosomes. Its phenotype strongly suggests that this plant should be considered as an amphidiploid. Another plant was found to contain 56 chromosomes; this plant was sterile and very feeble. During meiosis not only bivalents and trivalents but also quadrivalents were found. It is very probable that this plant is an autopolyploid. Soon after flowering this plant died. It is suggested that octopolyploidy is the highest polyploid form in *Phleum* which is viable.

219

Oliver, C.P. *The Relationship between Chromosomal Disarrangements and a Morphological Variant in* **Drosophila melanogaster**

Punch eye (*Pu*), a homogeneous dominant colour, inseparable from a translocation involving chromosomes 2 and 3, was reversed to wild type by the irradiation of *Pu*/*Cy* males. One reversed (Pu^{rv}) male was fertile, retained the 2-3 translocation and involved neither *X* nor 4. Some young Pu^{rv} flies have a homogeneous brownish eye colour. Variegation has been observed only once.

Pu and Pu^{rv} balance with *CyD*. Both involve loci between *h* and *cu* on 3, and to the right of *Bl* on 2. Any chromosomal disarrangement associated with the reversion does not appreciably modify crossing-over.

The crossing-over percentages for the respective regions of *ru h th st cu sr Pr* are:

Controls	24·2	18·8	0·0	2·0	8·4	26·8
Pu	14·6	1·7	0·0	2·5	10·4	33·8
Pu^{rv}	11·4	1·1	0·05	2·1	12·9	31·6

with totals respectively: 462, 1173, 1578.

Percentages for *al dp b Bl c pr sp* are:

Controls	14·5	30·0	6·4	15·9	24·3	3·5
Pu	7·6	35·3	8·1	0·7	0·0	0·0
Pu^{rv}	9·1	39·6	6·9	0·3	0·0	0·0

with totals respectively: 875, 1218, 1204.

Yet a new chromosomal disarrangement apparently did occur with the reversion. Although *Pu*/*CyD* females mated to *S Pu Pr*/*CyD* males produced exceptions, separating *S* from *Pr*, with a 32 % frequency, CyD/Pu^{rv} females mated to *S Pu Pr*/*CyD* produced *S Pu Pr*/*CyD*, Pu^{rv}/*CyD*, *S Pu Pr*/Pu^{rv}, and only one *CyD*/*Pr*, one exception in 566. Also Pu^{rv}/*CyD* females mated to *Pu*/*Bl MC*3 gave no evidence of non-disjunction of fragments.

Both *Pu* and Pu^{rv} are homozygous lethal. The *Pu*-lethal reverted to not lethal and a new one developed. The compound *Pu*/Pu^{rv} is very viable but sterile, and is frequently associated with opaque wings, thin bristles, dark trident, and rough eyes. The eyes are very dark regardless of roughness and seem to be homogeneous. However, when fixed in alcohol, the eyes often develop light areas, indicating variegation. Light areas can occasionally be observed in the living eye provided proper shading is used.

The results cannot be given as evidence against position effect. Fragmentation occurred simultaneously with *Pu* and probably with Pu^{rv}. The fragmentations connected with Pu^{rv} occurred within the *Pu* disarrangement, and did not involve reversions of those loci. The mutation did not necessarily occur at *Pu*. Another locus involved in eye pigmentation (or one of Bridges's repeats) may have mutated, with this new balance counteracting *Pu*, to cause wild-type colour and a modification of the character which was lethal; the *Pu*-lethal seemingly was not a deficiency. Then the compound with its dark eyes will not be *Pu*/Pu^{rv}, but *Pu*/*Pu* plus the mutated gene in heterozygous form. This might explain the connexions between the same morphological character and chromosomal breaks occurring at varying loci, and explain changes in dominance of genes in fragments. In the present case it has not been possible to separate the loci and to determine whether the change involves *Pu* or a secondary locus.

220

Painter, T.S. *Salivary Chromosome Structure and the Genes*

Since the rediscovery of Mendel's laws the relation of cytology and genetics has been growing ever more intimate, so that, to-day, cytogenetic studies dominate much of the modern genetic work. Until recently, however, when the geneticist began to inquire into the physical nature of the gene, the microscopist could contribute very little from his observations in spite of the fact that the gene strings, or chromosomes, of hundreds of animals and plants had been studied with the greatest attention. With the discovery of the real nature of the salivary gland chromosomes this has changed, for we have here a material which has allowed the cytologist to formulate, and open up to experimental attack, many fundamental

questions about the nature of chromosomes and genes. I think, however, in fairness to the earlier workers, we should all realize that the development of the salivary chromosome approach was a direct outgrowth of the X-ray technique, initiated by my former colleague, Dr H. J. Muller, and ultimately rests on the work of the whole *Drosophila* School. For without broken chromosomes genetically analysed, we would not have been able to recognize the salivary chromosomes for what they are, and they would still be the cytological curiosities they were so long after their initial discovery by Balbiani in 1881.

It is, of course, the fact that specific genes are represented, directly or indirectly, by definite bands along salivary chromosomes which has been the point of central interest and of departure for innumerable studies which have now extended into many different fields. I shall discuss just one phase here, the structure of salivary chromosomes, especially as relates to the possibility that the chromomeres of the bands represent the genes, with or without accessory material, and the question of how salivary chromosomes are to be interpreted in terms of the elements we ordinarily see in mitosis or meiosis.

You are all familiar with the general appearance of salivary chromosomes. The bands are made up of transverse disks of chromomeres, which in any focal plane appear as rows. These chromomeres are often described from poorly preserved or otherwise unfavourable material, as granules or globules, etc., which gives us very little idea of their discreteness and their great diversity in form which is revealed in well-fixed and stained salivary chromosomes of a form like *Simulium virgatum*. This diversity is expressed, first, in size differences which range from a long diameter of about $0{\cdot}2\mu$ up to 0·8 or even $1{\cdot}0\mu$. In general, these size relations are constant and exceptions are easily understood. All but the tiniest chromomeres are visibly vesiculate and are made up of an outer hull of nucleic acid surrounding a protein centre. There is a great diversity in the texture of the hull and in its thickness; in some cases it appears very dense, in others flocculent or faintly granular. There is also a notable difference in the behaviour of the chromomeres during development of the salivary glands. All these differences, I must emphasize, are very constant and are of importance because they indicate a great diversity of chemical and physical make-up such as we would expect if the chromomeres are made up of genes.

The appearance of any band depends on the size and form of its individual chromomeres and their response to crowding. When the chromomeres are large so that they touch and crowd each other in the disks, the chromatin, which would otherwise be more or less evenly distributed about the vesicles, tends to be squeezed or, at any rate, deposited along the free edges of the chromomeres, forming two plates of nucleic acid separated by the protein vesicles. An appreciation of this fact is extremely important because each chromomeric disk, potentially at least, can form a double band, and the mere counting of the number of bands shown by a chromosome is not a sure index of the number of different chromomere disks. The crowding of the chromatin to the free edges tends to obscure small chromomeres which lie immediately adjacent to the larger units, and hence the compound nature of the band is not apparent until the chromosome is greatly stretched, and may not be easily visible even then. This not only explains why our earlier chromosome maps were incomplete, but probably also accounts for the apparent wide variation in the number of bands visible in different species of Diptera. Needless to say, before we can accept the latter as valid evidence against a gene-chromomere relation, the chromeric constitution of the various species must be critically appraised. Likewise in *Drosophila melanogaster* our estimates of gene number must rest on a tally of the chromomere disks or rows, and while the counting of bands is a useful index it is by no means an accurate method of determining the number of genes carried by a chromosome.

If we are going to attribute to the chromomeres of our fixed and stained chromosomes an important genetic role we may very properly inquire: Do they exist as such in living chromosomes, are they fact or artefact? In the earlier studies there was a difference of opinion on this point, primarily because in some species the salivary nuclei appear optically empty, but as it has turned out when salivary nuclei are examined through the body wall of normal living larvae, in *Chironomus* and in *Simulium* the chromosomes and chromomeres are distinctly seen, while in *Sciara* and *Drosophila melanogaster* they are not visible. Thus it is certain that chromomeres exist in living chromosomes and appear essentially as they do in fixed or stained preparations. In the living state optical differentiation seems to depend on the degree of hydration of the nucleus. For if one immerses an extirpated salivary gland of *Sciara virgatum* in hypotonic salt solutions the chromomeres swell and melt from view, but on return to normal or slightly hypertonic solutions the chromomeres reappear as before. This process can be repeated without apparent injury to the chromosomes.

Whereas chromomeres of various types are clearly visible in living nuclei the longitudinal threads which appear to connect the chromomeres of adjacent bands cannot be seen, nor are they usually visible as threads in preserved and stained lax elements. It is only when

the fixed chromosome is stretched somewhat that we see these fine strands, and some have questioned their reality in living chromosomes. I see no grounds for this scepticism in view of the protein nature of these threads. In living and in preserved lax chromosomes the bands are very close together and the fibres could scarcely be seen, if they existed as such, with a considerable space between each of them. It appears to me as probable that they really exist as columns of hydrated protein closely packed together in a transverse plane just as the chromomeres are, and only after dehydration or other shrinkage and a wider separation of the bands can they be distinguished.

One of the first questions asked, when the importance of salivary chromosomes was recognized was: Why are they so large? Studies directed towards a solution of this problem have not only led to a much clearer insight into salivary chromosome structure but have opened up new vistas in cytology. As you know, in attempting to account for the large size Bridges and Koltzoff, independently, suggested that salivary chromosomes represent completely uncoiled chromosomes which have undergone a number of longitudinal divisions without any fission of the nucleus. This multiple strand, or "polytene", concept has proved to be correct, but, paradoxically, it does not adequately explain either the great breadth or the great length of the salivary chromosomes in *Drosophila melanogaster*. The point is this: Whereas we only see 8 or 16 chromomeres and strands, in the fruit fly (more are reported visible with ultra-violet light), Hertwig showed that on the basis of salivary nuclear volumes we should expect to find 256 or 512 chromonemata. Following Hertwig's study many other observers reported or indicated a great discrepancy between salivary nuclear volumes (and thus the theoretical number of chromonemata) and the number of strands actually seen.

The cause for this discrepancy was unknown until the development of salivary chromosomes was followed through. Dr Griffen and I did this for *Sciara virgatum*. At the outset of development, salivary chromosomes have a simple chromomeric form, like any somatic prophase. The first step in differentiation is a great increase in the size of the individual chromomeres. After the chromomeres reach a large size they begin to divide, along with their connecting strands, and from this point onward nuclear growth in diameter is accompanied by an increase in the number of chromomeres and strands until the final stage is reached. This initial increase in chromomere size is a true growth process during which the original chromomere is reduplicated a number of times without a visible separation of the parts. Species appear to differ in the number of times the chromomeres may be reduplicated before an actual separation occurs, and thus in the number of chromomeres and strands visible in the end stage. In *Drosophila melanogaster*, for example, if the nuclear volume indicates that there should be 512 chromonemata, and we see evidence for only 8 or 16 chromomeres in each transverse disk, it follows that each of these visible chromomeres must be a cluster of 64 or 32 of the original units. The same considerations apply to the strands. This point is exceedingly important; clearly, the visible chromomeres in salivary chromosomes must be considered as compound, and must represent a cluster of closely appressed homologous chromomeres. If the chromomeres represent genes, more or less camouflaged, we are not looking at single genes but packets or aggregates of homologous genes.

It seems certain that much of the size of the chromomeres in fully differentiated salivary chromosomes is due to their compound structure, i.e. reduplication of the substance of the original ultimate chromomere, but it is extremely important to know to what extent the size is also due to the accumulation of accessory material or to changes in physiological activities. The answers to these questions are not known. Certain specific chromomere disks in *D. melanogaster* undergo a differential hypertrophy and form "puffed" regions. Since the chromomeric vesicular material is protein, one might suppose that it, like other proteins, is capable of large changes in volume due to the taking or giving up of fluids. And lastly, in view of the recently recognized process of endomitosis in other polyploid nuclei, we should expect that salivary chromosomes would exhibit a similar process during which the chromomere volumes might change. All this awaits investigation.

Considering now specifically the question: Can chromomeres represent the genes? let me summarize the pertinent evidence. Genes are arranged in a linear order along the chromosomes and judged by their effects, they are qualitatively different. The chromomeres, in turn, are arranged in a linear order along the chromosomes; they show a great diversity of morphological form, and a high degree of specificity in somatic synapsis indicating that they are qualitatively different; the absence of a chromomere is accompanied by the absence of a gene. And lastly the number of genes carried by *D. melanogaster*, as computed in different ways, and the number of bands on the salivary chromosome, are of the same general order of magnitude.

There remains the difficulty of chromomere size, which I think is vanishing with a clearer understanding of the physical and chemical nature of these chromomeres. When the multiple strand concept was first enunciated, it was quickly pointed out that the individual chromomeres could not be single genes because they had a different order of magnitude from

the largest known organic molecule, which was supposed to be far below the resolving power of our microscopes. But the recent work of Signer, Caspersson and Hammarsten and of Astburg and Bell indicates that molecules of nucleic acid are about 6000 A. long, which is 0·6μ, and chromomeres ordinarily show a long diameter of from 0·2 to 1·0μ. The width of the nucleic acid molecule is computed to be extremely small, 20 A., but the chromomeres are not single genes, but bundles of these lying, presumably, side by side, much like cigarettes in a package. The ability of proteins to take or give up water, thereby undergoing great changes in volume without a change in their chemical nature, may explain the width of chromomeres without assuming any other accessory material. These considerations, I think, give us ample latitude for reconciling the gene-chromomere hypothesis within such limits as the molecular physicists may impose.

I think that very few cytologists will question the fact that the giant salivary chromosomes show, on an enlarged and possibly a somewhat distorted scale, essential structures which exist in both meiotic and mitotic elements, but time does not permit me to more than summarize some views about the details of this relationship, so far as they are known. Somatic and meiotic prophases and salivary chromosomes are all chromomeric and form a progressive and related series expressed by an increase in length over all and an increase in the number of chromomeres. We have long recognized that the chromomeres seen in somatic prophases are not comparable to those of meiosis but rather are aggregates of the units seen in meiotic prophases. Do the chromomeres seen in the latter stage represent the elements of the separate disks of salivary chromosomes, are they really "ultimate" chromomeres as Belling thought? Unfortunately, exact data are lacking, forms showing meiotic prophases best have no salivary chromosomes and meiotic prophases in Diptera are almost undecipherable. I venture the opinion, however, that many meiotic chromomeres are compound because, first, in meiosis we do not see the wide range of size evident in salivary chromosomes and, second, in salivary chromosomes many non-homologous disks are so close together that the separation in the much shorter meiotic threads is extremely improbable. The evidence indicates then, that salivary chromosomes are extended pachytene chromosomes and the broader conclusion that the fundamental make-up of all chromosomes is chromomeric. And I think that at present we are entirely justified in considering the chromomeres as the gene-bearing portion of the chromosome.

Throughout this discussion the assumption is implicit that genes have a reality and exist as individual units no matter how they may be linked together. We are all aware of a second possibility, namely, that what we call a gene is simply a locus on the chromosomes where definite enzymes or other substances are produced by the interaction of what we might think of as non-specific organic compounds. The chromomeric concept would fit in with either hypothesis. In the solution of this broader question, as well as many others relating to the chemical and physical nature of the chromomeres and their connecting strands, we require the aid of physico-chemical methods and concepts, and we all realize that already an exceedingly capable group of workers from the physical sciences have joined hands with us. I feel very strongly, however, that our microscopic observations set a pattern of fact which should not be disregarded, and to which the physicists and chemists should make their interpretations conform if we are to make rapid and lasting progress together.

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PANSE, V.G. ***The Inheritance of Quantitative Characters and Plant Breeding***

The importance of the study of quantitative inheritance for a closer application of genetics to plant breeding has been recognized. The object of the present paper is to summarize the results obtained in a statistical study of quantitative inheritance relating to F_2 and F_3 progenies. The genetic and plant-breeding aspects of the results are emphasized.

The experimental data used refer to the staple-length measurements on F_2 and F_3 progenies of crosses between strains of cotton belonging to the species *G. arboreum* var. *neglectum*, grown at the Institute of Plant Industry, Indore, Central India. The regression of mean staple length of F_3 progenies on F_2 phenotypic values shows that it is advantageous to consider plot values and select individuals on the basis of their excess over the former where, as in the present case, interplot variation affects the character in addition to intraplot variation. The coefficient of regression also gives an estimate of the genetic fraction of the total F_2 variance. This is an important relationship since it affords a basis for separating the inheritable and non-inheritable components of variance in the experimental material.

The ratio of the square of the genotypic variance within F_3 progenies to the variance of this variance is shown to represent the "effective" number of factors which can account for the segregation in F_2 and which hypothetically possess equal variance and are without linkage. With a given F_2 variance and a given effective number of factors it is possible to set up different genetic systems or models consisting of factors

varying in magnitude and number and with or without dominance. Five models with the smallest possible number of factors or an infinite number and each with or without dominance are considered.

By the use of a moment-generating function in three variables the moments of the distribution of the F_2 phenotype and of certain related quantities are calculated for each system. With these it is possible to express in terms of the F_2 phenotype properties of the F_3 progenies such as the genotypic mean or variance, and further to calculate their mean values in a portion of the F_3 population resulting from a selected proportion of F_2 phenotypes. Similar mean values obtained from experimental data can be compared with these theoretical values in order to discover the presence or absence of dominance and to decide on the possible number of factors operating in the experimental material.

In the present case, assuming a 10 % selection in F_2, theoretical mean values for (1) the genotypic mean and (2) variance of F_3 progenies, (3) the covariance between the two, and (4) the variance of F_3 means, and (5) of variances are calculated for each model. Their usefulness for identifying the genetic situation and the information obtained from them on the effect of selection applied and on questions relating to further selection are discussed.

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PÄTAU, K. ***The Pairing Coefficient***

The frequencies of univalents, ring and rod bivalents, etc., are not simply determined by the chiasma frequency as such but by the frequency of pairs of arms connected with one another by at least one chiasma. The number of such pairs may be called *pairing number* $\bar{X}$. So long as every arm behaves as one pairing block $\bar{X}$ cannot exceed 2 in two or three homologous chromosomes and 4 in four chromosomes. The proportion of actual $\bar{X}$ to the potential maximum may be called *pairing coefficient* w. Under certain assumptions to be mentioned below the association frequencies can be calculated from w. Moffett's (1932) counts of quadrivalents, trivalents, bivalents and univalents in tetraploid cells of *Kniphofia* agree well with the expectation if w is equal to 0·82. In the complicated case of an aneuploid *Tradescantia* ($4n=2$, with two translocations) the frequencies of ten types of associations approximate to the expectation, though minor deviations suggest deviations from the assumptions.

These assumptions are: (1) complete pachytene pairing, failure of metaphase pairing being caused by failure of chiasma formation; (2) equal probabilities of each chromosome arm for making at least one chiasma; (3) no interference across the centromere (4) no "pairing interference" in polyploids, i.e. no correlation between choice of partner in both arms; (5) in polyploids: no change of partner within metaphase arms. At least a part of these assumptions is practically correct in some, and wrong in other cases. The analysis of association frequencies provides a method for the investigation of the problems indicated.

A tetraploid with highly significant agreement between observed and expected association frequencies would strongly favour the first assumption because otherwise at least slight deviations should occur. In triploids change of partner increases the number of trivalents while pairing interference has the opposite effect. Thomas's data of a triploid *Lolium* seem to prove pairing interference. Positive interference across the centromere can be measured by $I=1$ (observed variance of $\bar{X}$: binomial variance). Different probabilities in both arms for forming at least one chiasma (measured by the *inequality factor* $\alpha = w_1/w_2 \leqq 1$) have the same lowering effect on the variance of $\bar{X}$. So long as the two arms cannot be distinguished an observed $\alpha < 1$ may be due to either inequality or interference. Moffett's (1936) counts of association frequencies in tetraploid cells of *Culex* agree with the expectation if $\alpha = 0{\cdot}1$ and $w = 0{\cdot}52$. As *Culex* has about median centromeres such inequality seems very unlikely and strong interference must be assumed. In diploid cells I decreases from 1 to 0·12 with w increasing from 0·5 to 0·89, while the total chiasma interference remains strong. This suggests an important difference between the two kinds of interference and accounts for the absence of I in *Drosophila* which has a high w.

It can easily be seen that if a low chiasma frequency has a selective advantage both kinds of interference as well as inequality of arms must also be favoured.

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PATHAK, G.N. ***Studies in the Cytology of*** **Crocus** ***and Cereals with Special Reference to Satellites and Nucleoli***

Satellites and nucleoli have been studied in twelve species and two varieties of *Crocus* for the first time, except in *C. Olivieri* and *C. ochroleucus*, where satellites have been previously reported.

A new interpretation of the organization of nucleoli in plants has been suggested in *C. sativus* where the nucleoli arise as two bodies close together, one on each of the twin satellite threads of a telophase chromosome, thereby also showing conclusively the double structure of the chromosome at this stage. These bodies shortly fuse and form one globular

nucleolus. The number of satellites (2–6) corresponds in every species with the number of nucleoli in telophase. The size of the nucleoli also varies according to that of the satellites.

C. susianus was found to have twelve chromosomes and appears to be a secondarily balanced diploid with five as basic number and one pair of chromosomes reduplicated. This suggestion finds support from meiosis, where a ring of four chromosomes has been observed at diakinesis and metaphase. Prochromosomes have been found in many species, for the first time in fairly long chromosomes.

Triticum aegilopoides was found to possess two pairs of SAT-chromosomes, like *T. monococcum*. The number and size of nucleoli in telophase again corresponds to those of the satellites. On the hypothesis that a haploid complement has one satellite and one nucleolus, as has been demonstrated in many plants and animals, both these species may not be true diploids. This finds ample support from the irregularities observed by many investigators where these species were crossed with other *Triticum* and *Aegilops* species.

Oryza Eichingeri is found to be a tetraploid rice possessing forty-eight chromosomes, and eight nucleoli probably corresponding to the number of satellites. It is, therefore, probably a secondary octoploid.

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PATTERSON, J.T., STONE, W. and GRIFFEN, A.B. ***Crosses between Members of the*** **Drosophila virilis** ***Group***

This study was made on eight different stocks of *Drosophila virilis*. These fall into two general groups. One group centres around *D. virilis virilis* (Spencer) and consists of the standard *virilis* (Pasadena), Japan, China, New Orleans, and two strains from Texas. The second group consists of *D. virilis americana* (Spencer) and *D. virilis texana* (Patterson). Fertility between members of a group is fairly high, but is relatively low between members of the two groups. In spite of this low cross-fertility, some of all heterozygous types so far tested have been fertile. Genetic tests have shown that not all of the factors causing cross-sterility are the same in any two strains. In certain of the strains at least, some of these factors are recessive. When members of the two groups are crossed, the F_1 males and females occur with about equal frequency. Since members of both sexes are phenotypically normal and some are fertile, the general balance and sex determination is much alike in the two groups. Detectable morphological and physiological differences exist in several of the strains. The metaphase chromosome complex of the different strains varies from five pairs of rods and one pair of dots to one pair of rods, two pairs of V's and one pair of dots.

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PATZIG, B. ***Die Schizophrenie als genetisches Problem***

Alle Versuche, das Wesen und die Pathophysiologie der Schizophrenien von der klinischen und hirnanatomischen Seite her zu verstehen, haben bisher zu keinem Erfolg geführt. Die vergeblichen Bemühungen erklären sich einmal aus dem derzeitigen unzureichenden Wissen über die Hirnvorgänge im Allgemeinen und über die Stoffwechselvorgänge, ihre Anomalien im Gehirn und in den übrigen Organen, sowie über feinere Gefäss- und Zellveränderungen im Besonderen. In Anbetracht der Reversibilität der abwegigen Hirnprozesse bei dem schizophrenen Prozessgeschehen ist es schwierig, die klinischen und Stoffwechseluntersuchungen richtig anzusetzen.

Bei dieser Sachlage wurden für die Frage nach den ursächlichen Faktoren der schizophrenen Erkrankungen zunehmend erbbiologische Untersuchungen von Bedeutung. Diese ergaben, dass verschiedene Erbfaktoren am Zustandekommen dieser Erkrankungen beteiligt sind. Diese Teilfaktoren lassen sich nur durch eingehende klinischgenetische Sippen- und Reihenuntersuchungen erfassen, wobei neben den psychischen Veränderungen die somatischen Erkrankungen bei den Verwandten der Probanden besonders zu werten sind. Infolge des Aufspaltens müssen sich sowohl in der Ascendenz als auch in der Descendenz der Probanden diese Teilfaktoren nachweisen lassen. Hier kann die Erbbiologie helfen, ein klinisch undurchsichtiges Krankheitsgeschehen besser zu verstehen.

Auf Grund eingehender Sippenuntersuchungen kam ich zu der Auffassung, dass das Prozessgeschehen durch das Zusammenwirken eines dominanten Hauptgens und mehrerer Nebengene und Aussenfaktoren verursacht wird. Die Penetranz dieses Hauptgens, das sich heterozygot manifestiert, ist relative stark, die Expressivität sehr variabel. Es ist identisch mit dem Begriff des Schizoids und wurde dementsprechend als mutiertes cerebral wirkendes Allel aufgefasst. Als Nebengene dürften Mutanten in Frage kommen, die bestimmte Anomalien des Stoffwechsels und des Gefässsystems bedingen, daneben pleiotrope, striär wirkende Gene. Eine besondere Bedeutung dürfte den Aussenfaktoren—Infektionen und Intoxikationen—zukommen, die in sensiblen Phasen über das hormonale System und die Stoffwechselzentren wirken. Die Nebengene können

sich anscheinend bis zu einem gewissen Grade vertreten.

Bei diesen Sippenuntersuchungen liess sich relativ häufig eine an sich seltene Erkrankung, die Chorea minor (Sydenham), nachweisen: in 10 unter 48 Sippen = rund 20 %.

(Demonstration von Stammtafeln, die die Bedeutung des dominanten Hauptgens und das Auftreten von Chorea minor in diesen Sippen zeigen sollen.)

Betonung der den Schizophrenien und der Chorea minor gemeinsamen Faktoren, hinsichtlich der Auswirkung des Hauptgens, sowie der einzelnen Nebengene und Aussenfaktoren. Diese Ähnlichkeiten lassen an verwandte pathophysiologische Vorgänge bei der Manifestierung der Chorea minor und der Schizophrenien denken. Bei beiden Erkrankungen wirkt sich das Hauptgen cerebral aus, wobei der Wirkungsbereich des abwegigen Hirnmusters durch die jeweiligen Mutanten bestimmt wird. In diesem Sinne sind die Chorea minor und die Schizophrenien Hirnkrankheiten. Mit entscheidend für das Prozessgeschehen sind Aussenfaktoren, die in besonderen sensibeln Phasen wirksam werden.

Als ein häufig mit dem Hauptgen korreliertes Nebengen dürfte eine Mutante infrage kommen, die sich mesenchymal auswirkt und oft mit einer Stoffwechselanomalie verbunden ist. Diese Stoffwechselstörung ist an sich nicht krankheitsspezifisch. Erst durch die Verbindung mit dem Hauptgen erhält diese Mutante ihre besondere Bedeutung: Klinisch dürfte sich diese Verbindung als schizoide Psychopathie auswirken. Für das Prozessgeschehen kommt als weiteres Nebengen u.a. eine Allergie-begünstigende Disposition in Betracht.

Auf diese Weise dürfte es gelingen, die zahlreichen klinischen, chemisch-physiologischen und anatomischen Untersuchungen zusammenzufassen und die cerebralen Auswirkungen des Hauptgens unter Mitwirkung von Nebengenen und Aussenfaktoren zu verstehen. Damit gewinnen wir für die Pathophysiologie des schizophrenen Prozessgeschehens brauchbare Vorstellungen.

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PEKLO, J. *Relative Sexuality in* Fomes pinicola

For studies of relative sexuality, use was made of basidiomycetic sporophores of three species of *Trametes*, *Fomes pinicola*, and *Pholiota squarrosa*. A striking increase in the rate of copulation could be observed among monosporial mycelia derived from different sporophores (or different habitats). This leads either to the so-called "total copulating ability", when all the combinations of strains show positive reaction, or to "triangles", when copulation was observed among three strains, two of which may possess the same sign, + + or − −. Both these phenomena are explained by Kniep, Vandendreis, Bauch and others on the basis of "multiple alleles"; this theory can also be advanced to account for the so-called tetrapolarity of Polypori. However, in *Fomes pinicola* a phenomenon was observed which goes even further. Positive reactivity was observed among monosporial mycelia in one and the same sporophore, which can practically be characterized as "total copulating ability". All strains (with 5 % exceptions) copulated positively so that they may be assumed to be multiple alleles. Clamps observed in the line of contact between monosporial strains are considered as proof of the positive reaction. On further observation, however, it was discovered out of 267 positive reactions, 177, or fully 66 %, continued to produce basidia. If Kniep's interpretation be applied to this case, we will have to assume the existence of 500,000 multiple alleles for every 1,000,000 spores which a large sporophore can produce. The experiment was repeated four months later with another small piece taken from the same sporophore close to the first. The reactivity among the twenty-five strains, tested again by means of clamps, was undoubtedly much weaker, yet in certain lines, *4* (15+ :6−); *6* (13+ :6−); *10* (11+ :4−); *13* (10+ : 2−); *14* (9−10+ :1−); *20* (4+ :1−), it was so strong that, on the average, fully 70 % in these lines copulated. This also reminds one of the "total copulating ability" of the first series. Moreover, from 150 combinations, fully 135, or 90 %, showed here the "triangle" combination. This would lead to the conclusion that from one million spores of this series, 900,000 could be genetically associated by means of multiple alleles.

The limited range of these experiments does not permit us to draw exact conclusions as to the potency of such a large number of spores from the entire sporophore. It could be ascertained that in certain cases the theory of "multiple alleles" succeeded in interpreting the genetical basis of this type of copulatory activity. In order to explain the physiological basis (Hartmann), it draws our attention to combinations of small differences with which "multiple alleles" are frequently concerned. Consequently, in our case we are able to refer to slight quantitative differences (or to slight differences in the qualitative chemical composition) of sexual substances which distinguish strains of a fungus. But I doubt that in these two series of my experiments one could expect such enormous figures for a genetic basis of the "multiple allelomorph" type, and it would appear better to assume rather a series of *phenotypic* influences. Moreover, the reactivity among the strains

of my fungus is manifested in another way than by clamps, which lead only to the production of basidia. In lines where the ordinary clamps were missing, I found twistings of hyphae, and no basidia were produced; no cytological investigation has been carried out as yet. Nevertheless, in this case also it was possible to establish "multiple alleles" in triangles. Perhaps this type also belongs to reactions which contribute to the building up of sporophores. One can, however, recall two types of Bauch, found in the copulation of smuts.

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PENROSE, L.S. ***Maternal Age, Order of Birth and Developmental Abnormalities***

A positive association is demonstrable between maternal age and the incidence of Mongolian imbecility, gross malformation of the nervous system and central placenta praevia. The independent effect of birth order is not easy to demonstrate conclusively. Primogeniture, however, is likely to be a significant factor in determining the incidence of gross malformation of the nervous system and of congenital pyloric stenosis. The study of maternal age and birth order usefully precedes the investigation of the genetical backgrounds of these conditions. Mongolism and some other malformations may have their origins in chromosome anomalies. The underlying cause of congenital pyloric stenosis seems to be a recessive diathesis.

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PETO, F.H. ***Cytology of* Triticum-Agropyron glaucum *Backcrosses***

Tetraploid and hexaploid *Triticum* species can be readily hybridized with *Agropyron glaucum* ($2n=42$), but the F_1 is self-sterile. The basic cause of sterility is undoubtedly lack of homology between the chromosome complements, since only one to six bivalents plus an occasional trivalent are found at first metaphase. Although the F_1 hybrid florets are completely male sterile, seeds have occasionally been produced by fertilization with pollen of *Triticum vulgare*, *T. durum* and *Agropyron glaucum*. The chromosome numbers of the resulting plants closely approximate those expected if an unreduced female gamete were fertilized with a normal haploid male gamete (Table 1). If restitution nuclei were formed in the first division of the megaspore mother cell, the egg cells should be $2n$ and the resulting embryo $3n$. However, this is not the case, as all but two of the plants have from one to seven chromosomes less than the calculated $3n$ number. The most plausible explanation appears to be that cytokinesis failed in early anaphase of the second division and that slight irregularities of separation of half-univalents at first anaphase resulted in more or less than the unreduced chromosome number in the dyad restitution nuclei. Even though cytokinesis were faulty in second anaphase, it would probably not prevent the half-bivalents dividing, so that the total number of chromosomes in the resulting restitution nucleus would approximate the somatic number. Although it has not been possible to observe this phenomenon in megaspore mother cells, this explanation is nevertheless consistent with pollen mother cell behaviour in which the univalents lag and divide equationally at first anaphase and lie scattered throughout the nucleus at second metaphase, while the half-bivalents divide.

The above explanation does not agree with that proposed by Tzitzin, who also found that the backcross (Lutescens × *Agropyron glaucum*) × Lutescens gave progeny with 56 chromosomes. He observed that $7_{II}+28_{I}$ were present at first metaphase; the bivalents divided regularly and the univalents distributed at random. He assumed that an egg cell receiving all 28 univalents plus 7 half-bivalents was fertilized by normal wheat pollen. The principal objection to this explanation is the wide discrepancy between the mathematical chances of obtaining random univalent distributions of 0 and 28 (1 in 1·34 × 108) and observed floret fertility (1 in 700).

Three generations of the progeny of Mindum × *A. glaucum* and Lutescens × *A. glaucum* back-crossed to their respective wheat parents, have been examined cytologically. In the first generation of (Mindum × *A. glaucum*) × Mindum ($2n=49$), 8–11 univalents, 18–19 bivalents and 0–1 trivalents were found. Judging from the frequency of micro-nuclei formation in the tetrads, it might be expected that the univalents would be rapidly eliminated in succeeding generations. Contrary to expectation, the perennial plants in the

Table 1

Cross	No. plants	Observed chr. no.	Calculated chr. no.
[Mindum ($n=14$) × *A. glaucum* ($n=21$)] × Mindum	2	49, 50	49
[Mindum × *A. glaucum*] × *A. glaucum*	3	53, 54, 55	56
[Mindum × *A. glaucum*] × Garnet ($n=21$)	5	53 (1), 54 (3), 55 (1)	56
[Mindum × *A. glaucum*] × Reward ($n=21$)	3	53 (1), 55 (2)	56
[Lutescens × *A. glaucum*] × Lutescens ($n=21$)	2	56, 59	63

two succeeding generations were found to have chromosome numbers of 49–53, the univalents not being eliminated. It appears likely that the univalent chromosomes are mainly *Agropyron*, and since the genes for perennialism are to be found in these chromosomes, the perennial plants must contain these univalents. Consequently, this is an unusual situation, in which natural selection prevents a rapid return to meiotic and genetic stability.

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229

PHILIP, URSULA. ***A Genetical Analysis of Three Small Populations of* Dermestes vulpinus *F.***

Variations present in free-living populations are spread within each species according to its ecological habits. *Dermestes vulpinus*, a scavenger beetle, under the conditions found in storehouses, forms colonies inside bales of skins, which are stable for a number of generations. The genetical constitution of such populations is interesting to compare with the *Drosophila* ones so far investigated, which are in a constant state of flux.

During two successive years three small populations of *Dermestes vulpinus* from bales of different origin were inbred (sixty-two pairs). The animals showed a polymorphism, due to three pairs of allelomorphs inherited in a simple Mendelian manner (dark wing—light wing, black body—brown body, dark antennae—light antennae). "Brown body" was absent from one population of 283 animals and was not recovered on inbreeding twenty-three pairs.

Four further factors affecting the wing venation were present in all populations, but not showing openly in all of them.

Population 1937 contained in heterozygote condition "white eye", "short wing", and a factor causing the stiffening of the trochanter-coxa joint in the second and third pair of legs.

Population 1938 I yielded, besides two factors affecting the pattern of the white pubescence of the ventral side, probably a sex-limited autosomal character of systematic importance. The Dermestidae are subdivided into two groups as to whether the males carry a tuft of hair in a pit in the middle of the third or on the second as well as the third abdominal segment. *D. vulpinus*, though belonging to the first group, produced a second sex-pit on the third segment as a mutant.

In population 1938 II, a sex-linked lethal was found in one of eight families.

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PHILLIPS, R.W., SCHOTT, R.G., TERRILL, C.E. and GILDOW, E.M. ***Long-range Transportation of Ram Semen for Use in Artificial Insemination***

During three breeding seasons ewes were inseminated with semen shipped by air express from Dubois, Idaho, to Moscow, Idaho (700 miles), Beltsville, Maryland, to Moscow (2600 miles), and in both directions between Beltsville and Dubois (2250 miles). This work resulted from a desire to use certain outstanding sires at two experiment stations during the same breeding season, and it has served to demonstrate the possibilities of transporting semen over long distances with existing transportation facilities and laboratory techniques.

Semen, collected (1) directly from the vagina, (2) with the artificial vagina, and (3) by electrical stimulation of ejaculation, was placed in small vials under mineral oil and packed in vacuum bottles with ice and cotton. The time in transit ranged from 19 to 74 hr., and averaged 35 hr. During the 1938 season the temperature in the vacuum bottles at arrival was taken on all shipments. The range was from 0·5 to 9·0° C. and averaged 3·6° C. Upon arrival semen was stored in refrigerators at about 5° C. until used.

During the first two seasons ewes were inseminated only once and at varying times during the oestrus period, the general plan being to use the semen as soon after arrival as possible. In the third season ewes were inseminated 12 hr. after they were first observed in heat and again at 12 hr. intervals as long as oestrus continued, or until the immediate semen supply was exhausted. The dosage at each insemination was 0·2 c.c.

Data obtained on the semen of each ram for each shipment included volume of ejaculate, sperm per c.c., abnormal sperm per 1000, motility score at collection and on arrival at destination, and percentage motility at collection and on arrival. Wide variations existed in the quantity and quality of the semen produced, as well as in the results obtained from inseminations. No pregnancies resulted from the use of semen from seven rams, while that from others gave from 4 to 40 % successes.

Of the 309 inseminations, thirty-one resulted in pregnancies and thirty-six lambs were produced. Semen varied in age from 22 to 200 hr. when used. The greatest age of semen used successfully was 115 hr. No consistent trend was found in the proportions of success obtained with semen in the various ages from 22 to 115 hr. The various measures of semen quality were studied in relation to successful use of the semen, and a consistent trend was observed in only one criterion, the motility score on arrival. Of the other measures, none gave clear-cut indications of

the success with which semen could be stored and then used for artificial insemination. There is definite need for more work on methods of evaluating semen.

The number of inseminations and the pregnancies obtained are indicated below:

Breeding season	Stations	No. of rams used	No. of heat periods at which inseminations were made	Pregnancies
1936	Dubois to Moscow	1	28	3
1937	Beltsville to Moscow	4	60	5
	Dubois to Moscow	1	35	0
1938	Beltsville to Dubois	3	43	1
	Beltsville to Moscow	4	34	1
	Dubois to Beltsville	2	53	13
	Dubois to Moscow	4	56	8
	Totals	19	309	31

The results obtained indicate that the practical use of ram semen, where storage periods of one day or more are necessary, will be limited until techniques for storage in transit are improved. The variable results obtained from different rams indicate the desirability of using many rams in studies of semen quality and methods of storage, rather than basing results on a few individuals.

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PHILP, J. ***On Wheat Breeding and Genetics***

The application of genetical knowledge and experience to plant-breeding work in Egypt has been of great advantage in that it has produced positive results with a saving of time, labour and expense.

It led to efforts being concentrated first on selection within the long-established crops and within imported material of the relatively new crops. Improvements in yield, ranging from 7 to 38 %, and in other respects have thus been quickly obtained in wheat, barley, beans, maize, millet, broomcorn, rice, sesame, groundnuts and castor beans. Hybridization has also given successful results but has taken a longer time.

The basic principles of genetics were applied in the methods of hybridization, selection, and propagation of pure strains. Studies on small samples of large families, checked by general observations on subsequent generations, provided a valuable insight on the genetic constitution of the material. Calculations were made on the minimum number and size of the progenies which required to be grown, and pure strains were thus produced quickly and with very little labour. Families behaving in an exceptional manner were given special treatment if necessary, while conclusions could be drawn as to whether unexpected off-types followed from natural crossing, gene mutation, chromosomal aberration or accidental mixture and the methods were modified accordingly. Moreover, the information obtained on the genotype of parental varieties was used in later breeding work.

The commonest and most difficult task was to produce varieties of improved yield. Yield is mainly the result of a series of physiological processes which physiologists, or breeders themselves, must first determine before their genotype can be investigated. Developmental studies of Egyptian wheats have therefore been made and the results have been applied with advantage in hybridization and selection work.

Pure research studies have demonstrated the complicated cytogenetic behaviour of pentaploid wheat hybrids, and this knowledge has been a valuable guide in breeding for rust-resistant *vulgare* types from interspecific crosses.

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PLAGGE, E. ***Die Wirkung des Gen-abhängigen*** **a$^+$-*Hormons bei*** **Ephestia**

Die Versuche über einen gen-abhängigen Wirkstoff, das sogenannte a^+-Hormon, bei der Mehlmotte *Ephestia kühniella* betreffen eine Allelenreihe a^+, a^k, a, die quantitativ abgestuft in die Bildung der Merkmale der Pigmentierung von Raupenaugen, Raupenhaut, Hoden, Gehirn und Imaginalaugen eingreifen. Die dunklen Pigmentierungsmerkmale, die dem Gen a^+ zugeordnet sind, werden durch das a^+-Hormon ausgelöst, einen Stoff, der in a^+-Geweben gebildet wird. a-Gewebe färben sich, in a^+-Wirtstiere implantiert, a^+-gemäss aus. a^+-Gewebe färben sich in a-Wirtstieren autonom aus, und durch das von den Implantaten abgegebene a^+-Hormon werden die Pigmentierungsmerkmale des a-Wirtes ebenfalls a^+-gemäss ausgebildet. Extrakte aus a^+-Tieren, die in a-Tiere injiziert werden, rufen dort ebenfalls eine a^+-gemässe Merkmalsbildung hervor. Durch das Gen a ist die Bildung des a^+-Hormons unterbunden. Durch das Gen a^k wird die Bildung des Hormons nur teilweise gehemmt. Die quantitativ abgestufte Pig-

mentierung der Merkmale von a^+-, a^k- und a-Tieren ist also durch verschiedene Grade der a^+-Hormonbildung zu erklären. Die Wirkung des a^+-Hormons ist mit der Wirkung des v^+- und cn^+-Hormons bei *Drosophila* identisch. Durch Extrakte aus a^+-*Ephestia* und aus +-*Drosophila* werden sowohl die Augen von *a-Ephestia* als auch von w^a *v*- oder w^a *cn-Drosophila* ausgefärbt. Extrakte aus *v-Drosophila* sind in *a-Ephestia* unwirksam, desgleichen Extrakte aus *a-Ephestia* in *v-Drosophila*. Durch das Gen *v-Drosophila* und das Gen *a-Ephestia* fallen die Wirkungen des a^+-Hormons und des v^+-, cn^+-Hormonsystemes gleichzeitig fort. Das a^+-Hormon wird bei *Ephestia* durch verschiedene Gewebe gebildet, z.B., durch Augen, Hoden, Ovarium, Gehirn. Es ist während des ganzen Lebens wirksam. Die a^+-Merkmale werden zu verschiedenen Zeiten ausgebildet. Raupenaugen und Raupenhaut färben sich schon embryonal aus. Die a^+-Hormonbildung beginnt embryonal schon sehr früh. In heterozygoten a^+/a-Embryonen aus a/a-Müttern, die das Gen a^+ durch das Spermium bekommen haben, lässt sich das a^+-Hormon bereits in ganz frühen Stadien durch Extrakte nachweisen; die Wirkung des Gens a^+ hat also schon frühzeitig begonnen. Der Hoden färbt sich später in der Raupe, das Gehirn und das Imaginalauge in der Puppe aus. Entsprechend der verschiedenen Ausfärbungszeit haben die Reaktionsgewebe auch verschiedene sensible Perioden. a-Raupenhaut und a-Raupenaugen können durch das a^+-Hormon jederzeit ausgefärbt werden. Der Hoden ist nur bis zur Verpuppung reaktionsbereit, das Imaginalauge bis *ca.* 11 Tage nach der Verpuppung. Die Stärke der Reaktion in a-Geweben ist von der Zahl und der Art der a^+-Implantate abhängig. Im allgemeinen ist der Reaktionsgrad proportional zur Hormonmenge. Da a-Hoden durch a^+-Gehirnimplantate nicht ausgefärbt werden, wird in a^+-Gehirnen anscheinend ein anderer Stoff gebildet als in den anderen Hormonbildnern. Das a^+-Hormon wird in den Eischläuchen gespeichert, während Hoden das Hormon nicht speichern, sondern dauernd abgeben (schon in 24 Stunden eine für die Ausfärbung von a-Imaginalaugen genügende Menge). Die aus der Rückkreuzung a^+/a-♀ × a/a-♂ hervorgehenden a/a-Nachkommen haben a^+-gemäss gefärbte Raupenaugen und Raupenhaut, eine Folge des in den Eischläuchen der a^+/a-Mutter gespeicherten a^+-Hormons (Prädetermination durch das a^+-Hormon). Diese Prädetermination klingt im Raupenleben allmählich ab. Sie kann experimentell erzeugt werden: Wird a/a-Weibchen a^+-Hormon zugeführt, so zeigen die aus diesen Weibchen hervorgehenden a/a-Raupen ebenfalls eine a^+-gemässe Raupenaugenpigmentierung. Auch das Gen a^k bewirkt in a/a-Nachkommen aus a^k/a-Weibchen eine Prädetermination, die in ihrer Wirkung geringer ist, als die des Gens a^+.

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PLOUGH, H.H. ***The Influence of Temperature in Evolution as shown by Studies of Lethal Mutation in* Drosophila**

In general, temperature may be expected to influence evolutionary processes in three different ways: (1) character expression, (2) mutation, (3) selection. On point (1) our data, like those of Plunkett, Child, and Timofeef-Ressovsky, show very substantial effects of temperature changes during development on adult characters, as will be shown in a comparative table. Their chief importance in evolutionary change is that resulting from a shift from the recessive condition to that of partial or complete dominance. Thus changes in (1) find their evolutionary significance chiefly in the speeding up of the process of selection.

With respect to point (2), mutation, three sorts of effects of temperature are indicated. First, our data completely confirm those of Timofeef-Ressovsky on chromosome I, that a rise in temperature within the normal range causes a corresponding rise in mutation frequency in accordance with the principle of van't Hoff. Secondly, our data, together with the recent results of Birkina (1938), show that temperature shocks (short exposures to lethal temperatures above or below the normal range) also produce a small increase in mutation frequency. Since no species is genetically static, all these mutations would appear and be subjected to selection even without temperature changes. It is necessary to conclude therefore that, as for (1), the effects of temperature on mutation (2) are of no significance, except perhaps in speeding up the automatic genetic processes.

It is with respect to selection (3) in its influence on gene frequencies in populations that temperature can be shown to have important effects on evolutionary processes. In Wright's (1937) analysis it is shown (A) that in a large freely inter-breeding population all gene frequencies approach equilibrium, which will be disturbed by secular changes. These would lead to (B) large populations subdivided into many partially isolated groups, where random divergencies in gene frequencies make for continuous change by inter-group selection, and thus give the most favourable population for evolutionary progress. Finally, in small isolated communities (C) there is a tendency toward fixation of random combinations at dead levels.

We have tested the second chromosome lethal frequencies of five stocks of *Drosophila* from different populations. In two wild populations nearly half the chromosomes tested bore lethals (44·3 and 43·1 %). In the Lausanne stock culture the percentage was 0·0. Between these extremes appears a Florida stock with 5·4 % and Dubinin's Gelendzhik tests of

7·98, 12·66 and 8·78 % respectively. Dubinin's populations fall into class (B), showing an unstable equilibrium with few lethals and slight but constant change from year to year. Our New England wild stocks appear to be (B) transformed by seasonal temperature effects to (C). The low temperatures of the severe winters kill off most of the large summer population, leaving a series of isolated communities in which the frequency of lethals and other mutations may rise to a high point. Our various stock cultures also fall into group (C). In the latter cases, however, artificial selection has reduced the number of lethals and standardized the lines.

From these studies of lethal frequencies, we conclude that the specific effects of temperature on character expression and on mutation have at most the effect of slightly speeding the automatic selective processes, which may then come to a complete equilibrium in a large or a very small population. The chief influence of temperature in evolution appears to be its action as a secular agent in fortuitously killing off large portions of natural populations, thus converting them periodically into small discontinuous groups. This shifting of gene frequencies may be supposed to be an important factor in preventing equilibrium and in favouring continuous evolutionary change.

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Plough, H.H., Child, G.P. and Ives, P.T. ***The Importance of Temperature and Heredity for Mutation Frequency in*** **Drosophila**

The following are the facts brought out by our survey of the effects of temperature on mutation frequency, and the interpretations which we believe these facts justify. (1) The frequency of lethal mutations in all chromosomes of *Drosophila* is influenced directly by temperature and has a temperature coefficient of about 3. (2) Temperature shocks both above and below the normal optimum produce an increase in mutation frequency in certain stocks which is proportional to the severity of the shock. (3) There are clear-cut genetically determined differences in mutation frequency between different stocks. All the chromosomes in any one stock appear to be affected by the genes determining high or low mutability. (4) Temperature shocks increase the frequencies of lethal mutations in stocks which give low values at constant temperatures, while they produce no effect on those which give high values.

In general, the interpretations of these observations require the well-demonstrated framework of modern genetic theory. Unlike Goldschmidt we believe that there are "genes, gene mutations and wild type allelomorphs" as well as deficiencies and translocations. The ideas connected with position effect are no more difficult to fit into the current picture than was the apparent failure of mutation to show a temperature coefficient. The facts given seem to us to be best explained by the following provisional conclusions: (5) Gene mutations, and perhaps also small deficiencies, are chemical transformations showing a direct relation to temperature in accordance with the van't Hoff rule. (6) Other lethal mutations are due to small or large chromosomal rearrangements or aberrations, involving two breakage points. These show no temperature relation but are increased in frequency by temperature shocks. (7) The genetically determined differences in mutation frequency between stocks are apparently due to differing tendencies to chromosomal breakage in all the chromosomes. (8) Temperature shocks, or genes stimulating mutability, appear to act by changing the physical texture of the chromosomal framework so as to make it more subject to breakage.

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Pohlisch, K. ***Die Vererbbarkeit der Geisteskrankheiten***

Die Erbpsychosen werden zur Zeit noch in grosse Gruppen zusammengefasst als überwiegend klinisch gewonnene Formenkreise und nicht als genetisch gewonnene Erbkreise. Letztere zu schaffen besonders mit Hilfe von Zwillings- und Familienuntersuchungen, ist eine der wichtigsten Zukunftsaufgaben für die Psychiatrie. Für die jetzigen Formenkreise besitzen wir die eugenisch wichtigen Ziffern über die Erbprognose, Krankheitserwartung in der Bevölkerung, über die Manifestationswahrscheinlichkeit und Fruchtbarkeit. Für die Mehrzahl der Erbpsychosen steht die Kenntnis des Erbganges noch aus.

Aus den Phänotypen, d.h. aus den mannigfachen Symptomen- und Verlaufsgestaltungen sollen Genotypen hergeleitet werden. Die Bedeutung einzelner Einflüsse auf die Gestaltung der Phänogenese wird besprochen. Gifte, Infektionskrankheiten, Hirnvorletzungen machen grundsätzlich andersartige Psychosen als die erblich bedingten. Das gleiche gilt für Schwachsinn und Epilepsie. Wir können also in der Regel eine Geisteskrankheit als erblich oder als nichterblich erkennen.

Dem Manifestationsalter, dem sog. Zeitfaktor der Genetiker, kommt für die Erbpsychosen grosse Bedeutung zu.

An dem guten Modell der "Chorea Huntington" wird die Betrachtung der Erbpsychosen nach genetischen Prinzipien eingehend exemplifiziert. Es lässt sich Sicheres über Penetranz, Manifestationsalter und

sehr Wichtiges über die grosse phänische Variabilität aussagen. Bemerkenswerterweise treten beim typischen Manifestationsalter um das 35. Jahr choreatische Bewegungsstörungen auf, dagegen bei 20-Jährigen striäre Versteifungen und bei 60-Jährigen Intentionstremor, also andersartige Bewegungsstörungen. Die Chorea Huntington ist ein homogener Biotypus im Gegensatz zu den eugenisch so wichtigen *Sammelgruppen der schizophrenen und manischdepressiven Erkrankungen*. Bei den letzteren handelt es sich wahrscheinlich um heterogene Biotypen.

Die *kindlichen Schwachsinnsformen* sind ebenfalls heterogene Biotypen. Der Blick ist jetzt von der früheren ausschliesslich psychopathologischen Beurteilung des einzelnen Schwachsinnigen neben dem Sippenbefund auf neurologische und andere somatische Befunde, etwa auf Missbildungen, Störungen des Stoffwechsels und Störungen anderer Organsysteme gerichtet.

Das *Psychopathieproblem* befasst sich mit einer besonderen, eugenisch wichtigen, negativen Variante der Persönlichkeit.

Die so oft beobachteten *Missheiraten* von Minderwertigen aller Art untereinander sind eugenisch sehr zu beachten; für die genische Betrachtung stellt sich leider dies Problem als kompliziert heraus.

Die Individualpsychiatrie ist zur Sippenpsychiatrie erweitert werden. Zu diesem Zwecke wurden in Deutschland umfangreiche und weit differenzierte Organisationen geschaffen, die besonders der *positiven Eugenik* dienen. Die Förderung der durch den Sippenbefunde als erbbiologisch und sozial vollwertig oder hochwertig erkannten Personen hat sehr viel grösseren Umfang angenommen als die Sterilisierung erblich Geisteskranker.

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PONTECORVO, G. ***Problems in Connexion with the Selection of Beef and Draft Cattle***

Beef and draft cattle are characteristic of farming conditions usually associated with high densities of human settlement, difficult topographic and soil conditions, and systems of cultivation requiring much animal labour. They have generally been evolved by development of beef qualities in primitive, hardy draft types (such as the present-day Podolian, Hungarian, Maremmana, etc.) associated with a progressive amelioration of the agricultural environment. At the lowest stages of discontinuous farming and extensive unimproved grazing lands the work is done entirely by oxen, the cows range freely and are used solely for breed replacements, beef is only a by-product from aged animals. At higher stages, with closer settlement and high densities of both human and cattle populations, the work is done by stabled cows, and those males not necessary to reproduction are used for beef production. All intermediate stages exist, but the conditions for increasing the proportion of working females to males (replacing the working males by working females) are those of an increased density of cattle population, so that the labour demands can be distributed over large numbers of working females. Data from Tuscany (central Italy), where agricultural conditions are very variable within a limited area, show that the density of the cattle population and the ratio of working cows to oxen are closely interdependent.

Under such environmental conditions, a high degree of genetic variability is desirable in the bovine population, with regard to both beef and draft performance. On the other hand, at higher levels of agricultural settlement and of cattle density, where only the cows are worked, a genetic improvement in these characters must take place, so that good draft cows may give sons with high beef-producing capacities.

Since individuals with beef-producing and draft capacities associated do exist, the incorporation of the two in one animal is therefore *physiologically* possible. Nothing, however, is yet known as to the possibility of *genetic* fixation of the association, as these cases may be only successful heterozygous combinations. The main difficulty of a plan of improvement depends on (*a*) the lack of definite record of performance standards both for meat and for draft; (*b*) the necessity of using meat-producing capacity of the male offspring prepared for slaughter, in evaluation of the parents, which are reared under different conditions.

Details are given of the "nucleus plan" used in Tuscany for the last five years, the criteria adopted, and some preliminary results. Live weights and growth rate of calves are of low variability, the hereditary portion of the variance probably being very low; the necessity is emphasized of testing these important factors under standard conditions. The same applies to draft ability.

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POULSON, D.F. ***The Developmental Effects of a Series of Notch Deficiencies in the X-chromosome of* Drosophila melanogaster**

A number of Notch deficiencies of different sizes (all producing the same phenotypic effect in heterozygous females) has been investigated embryologically to discover the fate of the Notch males which do not appear as adults. Although some differences exist, the principal embryological upsets in the four Notches

(N 264–38*a*, N 8, N 264–19*a* and N 264–8*a*) are essentially the same. A germ band is formed, extends, and shortens. The embryonic membranes spread out to cover the dorsal side of the embryo. Normally, the nervous system and hypoderm are sharply distinguishable at this time, but in all of the Notches there is no separation of superficial cells from the neuroblasts, and all of the ventral cells form part of an abnormal nervous system. This is likewise true of the cells on the dorsal side where the supra-oesophageal ganglia arise. Apparently many cells which would normally form mesodermal derivatives become part of this abnormal nervous system. There is little or no differentiation of tissues or structures of mesodermal origin. Mid-gut rudiments, although present, do not unite to form a complete mid-gut. Although hind-gut and malpighian tubes are present, the stomodaeum shows little development. None of the ectodermal derivatives of the anterior end, such as salivary glands or imaginal disk invaginations, appear. The cells which would normally form them become part of the mass of abnormal nervous tissue. Further development is entirely abnormal. The over-all effect is the development of ectodermal organs at the expense of others. Of the ectodermal structures the nervous system takes the ascendancy and does not give it up. It fails to become delimited, and the hypoderm fails to differentiate. This is in agreement with the fact that the Notches are cell lethal in imaginal hypoderm.

The facts outlined indicate that the embryological as well as the phenotypic effects of the various Notches are highly localized. The principal effects in the large deficiencies are attributable to the same locus which is either absent or inactivated in the others, the region of band 3C7. It is indicated that this locus comes normally into activity before any of the others in the large deficiencies.

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PRAWOCHEŃSKI, R. ***Some New Lethal Factors in the Horse***

Three lethal conditions recently observed in the horse are described. The first (already published) consists in crippled forelegs with crooked immobilized phalanges. When both forelegs are affected, the foal is unable to stand and to suckle. The condition was observed in a half-bred stud, where nine out of nineteen foals sired by an Anglo-Arab stallion were affected; unfortunately no data are available for his other progeny. A mare, Pututu, gave birth to three crippled foals in three successive years and had to be culled from breeding. This mare was the only viable foal produced by her dam, all her five sibs having crippled forelegs. Pututu and other dams of affected foals have a common ancestry.

The second defect noted is umbilical hernia. Among foals sired by the half-bred stallion Manfred, four foals out of the mare Peri at an Anglo-Arab stud, as well as foals out of other privately owned mares, were affected, while during the two years that another stallion was used, no defective foals appeared.

The third defect is the absence of eye orbits. Two cases have come under the author's observation. One was an Orlov foal descended from ancestors exhibiting various grades of blindness. The other foal was a thoroughbred, in whose ancestry occur two blind mares, viz. the dam of the famous stallion Dark Ronald, and that of Friar Tuck. The author believes that absence of orbits may be the ultimate expression of a complete polymeric series, whereas when only some of the factors are present, the condition is less severe, e.g. blindness or weak sight. Crippled forelegs are also thought to be based on polymeric factors. Both these characters are apparently recessive. It is emphasized that careful selection and control of health and constitution represent the primary task of modern animal breeding, since domestication favours undesirable mutations.

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PRICE, B. ***An Interpretation of Differential Birth-rate Statistics***

A more complete picture of differential fertility than that usually available was sought while holding a fellowship of the Social Science Research Council in Moscow during 1934–6. The group investigated was comprised of 282 urban families, sampled over the full range of occupations and status. As complete mental test and interview data as possible were secured for this population. The data on 260 of the families were sufficiently complete for inclusion in the study of factors affecting fertility.

Number of births was related to four variates, for each of which the parental averages were used. The variates were parental age at birth of first child, years of education, a composite estimate of social status, and test intelligence as measured by orally given synonym-antonym forms and Army alpha number-series-completion forms.

Fertility correlated negatively with all of these, and somewhat more markedly with the age and education variates than with status and intelligence. The intercorrelations for education, status, and intelligence were over 0·70, and the correlations of these variates with the age variate were low but significantly positive.

These findings are seen to reflect largely the costs to education, status, and *test* intelligence of early family

starting. For populations showing these relationships it appears difficult to believe that genetic selection against factors related to intellect is proceeding even as rapidly as genetic selection against factors related to self-interestedness.

As well as the possibility that there was "something about the nature of the education" of those of better status which reduced their fertility, it appears no less likely on the basis of the data available that, independently of their intelligence, there was something about the educated groups themselves which disposed them in the first place to be infertile. It would seem impractical to set out to shift birth-rate differentials while giving emphasis chiefly or only to the first possibility.

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Price, J.R. ***The Rate and Sequence of Gene-Controlled Chemical Processes***

In studying the inheritance of the sap-soluble pigments we are concerned mainly with two classes of substances, the anthocyanins and anthoxanthins, which are closely related to one another chemically. The anthocyanins vary amongst themselves with regard to the number of phenolic hydroxyl groups in the molecule, the nature and position of attachment of the sugar residues, and the methylation of hydroxyl groups.

The presence or absence of anthocyanins, the amount in which they are produced and the structural differences referred to are genetically determined. That is, the phenotypic expression of genes modifying flower colour is the result of certain definite and simple chemical reactions, and as such must be subject to physico-chemical laws. The expression of these genes at any given time will clearly be dependent upon the rate at which the chemical reactions take place. Consideration of reaction velocities is of the greatest importance, particularly with regard to competition. When one starting substance is utilized for two reactions, then the relative amounts of the products of these two reactions will depend on the rates at which they proceed.

The flower pigments provide many examples of competing chemical processes which are simplified if considered in the light of reaction velocity. In certain cases the main anthocyanin is contaminated with small amounts of cyanidin derivative arising from the non-completion of oxidation or reduction stages. In other cases, such as *Primula sinensis*, an apparently anomalous behaviour can be explained by competition between oxidation and reduction processes taking place at different speeds. The formation of certain classes of glycosides may also be incomplete.

In addition to competition in the synthesis of any one group of substances there is competition between different groups—the anthocyanins and anthoxanthins. This is exemplified by *Primula sinensis*, and in *Dahlia variabilis* we have competition between three classes of pigments. On account of the functionally tetraploid character of *Dahlia*, this plant shows dosage effects which enable us to establish the simultaneity of action of competing processes.

The sequence of action of the genes involved in the production of any substance is not easy to determine, but it is possible to determine it when more than one end-product is involved.

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Pybus, F.C. and Miller, E.W. ***Hereditary Bone Tumours and Oestrone***

By selection and inbreeding, a strain of mice with a high incidence of spontaneous bone tumours has been developed from Simpson Strain 3.

The bone-tumour strain has been inbred for sixteen generations, and bone-tumour incidence has risen from 1 % in the parent stock to an average of 44·7 % in the inbred strain. There is a marked difference in the sex incidence; 67 % of the females and 23·4 % of the males have neoplastic bone changes. Over 300 cases of such changes have occurred, from the earliest intra-osseous alterations (proliferation of osteoblasts with osteogenesis) to gross spindle-celled and osteogenic sarcomata.

The sex difference in incidence has led to a series of experiments with oestrone in which bone-tumour strain mice of different ages and from different lines and also mice from other inbred strains are being used.

In the bone-tumour strain, implantation of oestrone tablets causes widespread multiplication of the osteoblasts, and the whole bone is occupied partly by giant-celled tissue somewhat resembling osteoclastoma and in places producing cysts, and also by osteogenic tissue which produces definite osteomata. Spontaneous fracture also occurs. Painting with oestrone produces similar changes but there is a greater amount of osteogenesis.

Recent results show a difference in the reaction to oestrone of the bones of four inbred strains, comparable with the difference found in the reaction of their mammary glands. Aged mice from the bone-tumour, Simpson, CBA, and Edinburgh strains were implanted with tablets, after removal of the left tibia as a control. Typical changes were seen in the bones even after nine days. Simpson mice reacted to about the same extent as mice from the bone-tumour strain; changes were less widespread in the Edinburgh mice,

and slight in the CBA. Some of the latter are still living after two months; the others (of all strains) succumbed after much shorter periods.

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QUELPRUD, T. ***Variability and Genetics of the Human External Ear***

The human auricle is a rather complicated organ; the variability and heredity of its individual parts are now, however, through exhaustive twin and family investigations and studies of individual persons and embryos, clarified on a large scale.

Above all, the twin studies have shown the great importance of heredity in the building up of the different ear sections, be it in linear measures, angular measures, or in certain morphological characters.

For every individual part of the ear the best suited method of classification was worked out; then it was important to determine how far sex, age and right-left differences occur. It became evident that nearly all ear characters show at least one of these three differences. For almost all the linear measures one finds, for example, a sex difference; the males of all ages have a higher average. An exception is found in the length of the lobulus and the breadth of the concha, which are somewhat equal in both sexes. The linear measures always increase with age, but the rate of growth for each one of them is very different. The other characters are not homogeneous in their behaviour, but show varied developmental tendencies. For instance, the *Darwin's tubercle* is more distinct and frequent on the right side in both sexes, and with age it becomes more pronounced in men and less pronounced in women, while the *crus cymbae* is more frequent on the left side than on the right; it is more manifest in women and often indistinct in elder people.

In order to compare parents and children for the genetic analysis, corrections from unlike points of view were applied, so far as it was necessary and possible; sex differences too were considered.

The main results of the genetic analysis are as follows: Although the strong genetic influence on a series of characters could be demonstrated, a simple hereditary modus for most of them has not been proved. Nevertheless it cannot be said not to exist, because the variation of the gene manifestation due to fluctuating penetration and expression may distort the phenotype.

It can be emphasized that among the linear measures the ear breadth is eventually interpreted through a monofactorial scheme (intermediary behaviour), though this can be only an apparent result. Also the adherence of the ear lobe might be explained from a monofactorial point of view, but after a necessary sex and age correction the adherent lobe, in contrast to earlier researches, is sooner found to behave as dominant.

Simple inheritance among others is shown by the following characters:

(*a*) More or less completely dominant: fistula auris congenita, crus cymbae, crus anthelicis in cymbam, auricular drops and certain ear deformities.

(*b*) Recessive: tuberculum anthelicis, tuberculum helicis fossale, crus anthelicis tertium and band-like *Helix*.

Though proportionally few ear characters are known in their hereditary modus, one may not forget that for the others a series of facts also exists. The degree of hereditary influence is known, as well as the age and sex differences and other such variable factors and the probable expectation from fixed parent combinations.

The human auricle, therefore, can now be suitably utilized for hereditary biological examinations, e.g. for twin diagnosis and inheritance tests.

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QUINTANILHA, A. ***Genetical Work on Basidiomycetes***

In the Ascomycetes, as well as in the Basidiomycetes, the phenomena of compatibility and incompatibility between different haplonts are hereditary; one pair of Mendelian factors (Aa) is responsible for the bipolar heterothallism, two pairs of independent factors (Aa, Bb) determine the tetrapolar one. These factors exist in nature in allelomorphic series, often with numerous terms, and mutations of these factors have been obtained in the laboratory under the control of tetrad analysis.

The presence of the same factor on two nuclei leads to a repulsion between these two nuclei; the intensity of this repulsion is greater in the pair (Aa) than in the pair (Bb); it grows in (Bb) with the age of the mycelia; moreover, the intensity of the repulsion varies also according to the nature of the elements of the same pair. It has always been impossible to overcome the repulsion between nuclei possessing a common factor of the pair (Aa); it is, however, easy to obtain regularly dicaryons from incompatible nuclei possessing a common factor (B) or (b).

The carpophores obtained from these illegitimate copulations are "chimaeras" where, besides apogamics bearing monocratic tetrads, there are others which are binucleate, caryogamic, producing dicratic tetrads.

On the other hand, there is an attraction between

compatible nuclei without any common factor; the intensity of these attractions varies according to the different possible combinations. A haploid nucleus placed in the presence of two kinds of compatible nuclei will select for mating one of the two, always the same one. The attraction between nuclei from interfertile geographical races is stronger than between nuclei from the same race; this facilitates the crosses and makes difficult the progressive isolation of races and varieties.

Everything happens as if our series of allelomorphic factors of compatibility were sex factors arranged according to their relative numerical valencies. Nevertheless, in spite of all the analogies between these phenomena of compatibility and the sex manifestations of living beings with haplogenotypical determination of sex, we are convinced that there is no homology between the two groups of phenomena. The heterothallic Ascomycetes as well as the Basidiomycetes must be considered as monoic species where the mutational introduction of sterility factors gave rise to bi- or tetrapolar heterothallic phenomena simulating sexuality.

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RACE, R.R., TAYLOR, G.L. and VAUGHAN, J.M. ***A Genetic Investigation of Acholuric Jaundice***

An account will be given of a joint investigation, undertaken by workers in haematological and genetical laboratories, of families in which occur cases of the blood disease acholuric jaundice. The essential underlying abnormality of this condition is a diminished resistance to haemolysis, or increased fragility of the red blood cells.

Though the disease is generally believed to behave as a dominant Mendelian character, in many of the families hitherto published there has been a preponderance of normal children from matings where one parent was a sufferer. In these families it would be expected that the affected children would equal the normal. It was thought that the explanation probably lay in the fact that many of the published pedigrees are based on clinical examination only. This is misleading owing to the presence of a fairly common latent form of the disease in which there are no symptoms nor signs of the abnormality, which can only be shown to be present by an elaborate investigation of the blood. Even when this has been done mistakes have arisen owing to the use of an insufficiently delicate technique. A more accurate quantitative technique has now been elaborated which has been used throughout our investigations.

Of special interest has been the question of the existence of so-called "acquired cases" in which both parents of a sufferer were free from the abnormality. If such cases did occur, too frequently to be explained by mutation, could any genetic light be thrown on their nature by a wider examination of their relatives?

In the hope of detecting linkage relations, if they exist, between the gene for acholuric jaundice and any of the recognizable common human genes we have examined all the members of our series for the following characters:

Blood groups *ABO* and *M* and *N*.
Ability to shed the *ABO* factors in the saliva.
Ability to taste phenyl-thio-carbonide.
Iris colour.
Attachment or not of the ear lobes.
Colour of the hair.

An account will be given of the families examined up to the time of the Congress.

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RAMIAH, K. and KADAM, B.S. ***Genic Symbolization in Rice*** **(Oryza sativa)**

The paper deals with the existing confusion in the description of characters of the rice plant and in the symbolizing of the identified genes responsible for these characters. The author has, after reviewing all the published literature on the subject, drawn up a list of the genes studied and a standard form of symbolizing them. The prepared list has been circulated to all the Rice Geneticists in various countries and the final agreed list will be published.

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RANGANANTHA RAO, V.N. ***Hybridization between Two Hybrids***

India was once famous for her cotton and cotton fabrics. Investigations made on a piece of cloth spun about 5000 years back found during the excavation at Mohenjadaro revealed the fact that cotton cultivation was at a very high level in India between 3000 and 2000 B.C. It is surmised that the variety of cotton then grown was *Gossypium arboreum* belonging to the Old World group. This variety is not in general cultivation at the present time. This plant, which possesses showy red flowers, is occasionally found growing near temples or as an ornamental garden plant. It has a long and silky staple but the ginning out-turn is poor. Efforts were made to combine the long silky staple of *arboreum* with long big bolls and high ginning outturn, the bolls of *arboreum* being small. The requisite

strains could only be had by resorting to hybridization. The parents used were two recently developed strains, one of them being an interspecific hybrid, *G. arboreum* × *G. herbaceum*, and the other an intervarietal one, *G. cernum* × *G. obtusifolium*. As a result of this complex cross three very promising strains in a homozygous condition have been isolated as early as in the third generation. These have been breeding true to the three characters, viz. leaf shape, colour of the petal and colour of seed. Samples of these when subjected to fibre test showed a close resemblance to that obtained from the cloth excavated at Mohenjadaro.

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RASMUSSON, J. ***The Field Trials in Sugar-beet Breeding***

Breeding work for practical purposes generally aims at producing varieties which give good average results of yield and quality when grown under very varying conditions. This is especially true for the sugar-beet which, being a cross-fertilizing plant, will generally react to breeding under specialized conditions in such a manner that in some few generations it is markedly adapted to those conditions, and this is often followed by the unwanted result that the strain is not fit for other conditions.

In order to counteract these phenomena certain precautions should be taken by the breeder in his field testing work. First of all, the variation in soil and climate within the area where the new varieties will be grown should be considered, and the field tests of the breeder should cover the main variations in these conditions. The differences between years in weather and agricultural conditions must also be thoroughly considered. Since the breeding of a new variety, even in sugar beet, covers only a comparatively short period and of necessity a different period than that in which the new type is to be used in agriculture, it is necessary to try to find means of representing in the trials these variations too.

In the author's own work these questions have been solved in the manner that within each field experiment with breeding material, sowing time, nitrogen fertilizing and harvesting time are varied. All material is subjected to those types of tests. No absolute treatment replications are made in one experiment, but the number of variety replications is slightly increased. Experiments of this type are carried out in seven very different places (varying in climate, soil and agricultural habits). In each experimental place initial selection is made. The types which in two or three successive tests have given good results at one testing place are then tested in all the different places.

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RASMUSSON, J. ***Quantitative Inheritance in Root Crops***

The main interest in quantitative inheritance in root crops has hitherto been confined to questions of inbreeding and outbreeding and of correlations between different characters. The beets (and mangels), swedes and turnips will be considered.

Inbreeding is as always the most effective means of producing a separation of different genotypes or rather gene mixtures. Close inbreeding even for a small number of generations seems to have such a deleterious effect on vitality and yielding capacity in all root crops that it cannot be taken into consideration for direct breeding purposes. Inbreeding can, however, be used as a breeding method by growing progeny obtained from selfing single plants or crossing pairs separately from everything else. Cases are known where these methods have yielded good breeding results. Even the slight inbreeding which occurs when mother plant families constitute the breeding units will in the long run have decidedly bad effects on vitality. Where the main breeding problem is not one of general productivity, inbreeding can, however, be of value in separating special types, for instance those resistant to certain diseases. On the other hand, outbreeding, i.e. crossing of material which is definitely unrelated, seems generally in root crops to have good effects on both productivity and general vitality.

CORRELATIONS BETWEEN CHARACTERS

Quality in root crops, especially in the sugar beet, depends largely on certain characters of a chemical nature. Several of these characters, as for instance sugar percentage, content of mineral salts, etc., are nearly always found to be correlated with size of the root. There are also some correlations between shape of the root and its chemical constitution. These correlations are partly of a modificative nature, but they also depend partly on genical causes. These should probably be interpreted as linkages between the genes responsible. So far as the investigations go it seems that the correlation caused by linkage is the more effective for the purpose of selection. So, for instance, selection for sugar content alone will decrease not only root size but also sugar yield much more than would be expected from the usual weak correlation found on analysing roots of any variety grown in a small area. There are also indications of a negative correlation between yield of roots (or dry matter) and yield of seed. The correlations mentioned seem open to attack and to breaking up, probably because the linkage is not too strong. The linkages between root

shape and quality in sugar beets and mangels seem, however, to be fairly strong as they have proved difficult to break.

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RAYCHAUDHURI, S.P. ***The Validity of the Bunsen-Roscoe Law in the Production of Mutations by Radiation of Extremely Low Intensity***

Inseminated females of *Drosophila* were placed on syrup food in a cooled incubator at 8° C. for a period of 30 days, during which they were continuously subjected to the γ-radiation from 70 mg. of radium, at distances at which the incident radiation amounted to 0·01 and 0·05 r. per min. for lots *a* and *b*, respectively, giving total doses of 400 and 2000 r., and another lot, *c*, was irradiated for 45 hr. at a distance giving 0·8 r. per min., the total dose here also being 2000 r. Controls were maintained for 30 days in the same way except for the lack of radiation. After the 30-day period the females were allowed to deposit their eggs, and the flies from the latter were tested for sex-linked lethals. The results were: controls, 3471 cultures, 11 lethals; lot *a*, 3855 cultures, 59 lethals; lot *b*, 868 cultures, 58 lethals; lot *c*, 762 cultures, 40 lethals. Subtracting the control frequency, it is found that these represent mutation frequencies, per 100 r. of total dose, of (*a*) $0{\cdot}30 \pm 0{\cdot}04$ %, (*b*) $0{\cdot}32 \pm 0{\cdot}04$ %, and (*c*) $0{\cdot}26 \pm 0{\cdot}04$ %.

Since previous work of Timoféeff-Ressovsky and others had established the induced mutation frequency of 0·30 % per 100 r. for intensities from 10° to three times 10^2 r. per min., it is seen that the present work almost doubles the tested range of applicability of the Bunsen-Roscoe law. Moreover, at these low intensities the principle of linear proportionality of effect to total dose is seen to hold also, and the results are the same for γ as would be expected for X-rays. Since at 0·01 r. per min. there is on the average only one ion pair produced in a sperm nucleus every 27 min., and since the ion pairs produced by γ-rays are rather far apart, it is now more difficult than ever to avoid the conclusion that individual mutations arise from individual ionizations and that there is no threshold intensity.

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REED, S.C. ***Interaction between the Autosomes of* Drosophila melanogaster *as Measured by Viability and Rate of Development***

Females of an inbred *al c*; *se ss*; ey^R strain were crossed with males from a "wild" strain which had been inbred (brother × sister) for over sixty generations. The F_1 males, in which of course there was no crossing-over, were mated with mutant strain females. The backcross offspring were expected to appear in eight genotypes with equal frequencies were there no differences in viability. The marker genes permitted scoring each fly as to whether it was heterozygous or homozygous for each of the mutant autosomes.

The genes used as markers probably have a distinct negative effect upon both viability and rate of development, but one of the autosomes (markers *al* and *c*) increased viability to a greater extent than did the wild-type heterozygote. Apparently the possible negative effects of *al* and *c* were more than offset by other genes on this autosome which had positive effects. The negative effects of the homozygous mutant third and fourth chromosomes were severe.

The interactions of the one positive and the two negative autosomes in the eight genotypes were of some geometric order. It was found that the addition of a positive or negative autosome to any genotype will cause a change in viability in the *direction* of the added autosome, but the *amount* of change is at present unpredictable and depends upon the particular combination to which the autosome was added.

The relation between the different autosomes and the rate of development of the fly was quite different from the relation between autosomes and viability. The second chromosome (marked by *al c*), which gave the only positive contribution to viability, retarded development more than either the third (*se ss*) or the fourth (ey^R). The effects of the three autosomes on rate of development were not strictly additive.

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REED, S.C. and HENDERSON, J.M. ***Determination of Hair Pigments***

Transplantation studies with skin of black-and-tan mice showed that dorsal and ventral tissues are differently organized in relation to pigmentation. The cells of the dorsal and ventral tissues are apparently identical, but they are arranged in a different morphological fashion in the two tissues. This theory is dependent for its demonstration upon the migration of cells into the grafts. Cells migrating from dorsal tissue (which is potentially black) into grafts of ventral tissue will produce tan hairs; conversely, cells migrating from ventral tissue (potentially tan) into a graft of dorsal tissue will produce black hairs.

Various coat colours have recently been used with black-and-tan to prove that there is actual cell migration into the grafts. Dorsal black grafts on the tan chests of brown-and-tan mice are invaded by cells from the tan chest which produce dorsal brown

hair. Further, dorsal grafts from albino donors (which by testing were found to be genetically black-and-tan) were invaded by dorsal dilute-brown hairs when placed on the tan chest of a dilute brown-and-tan host.

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RHOAD, A.O. ***A Method of Assaying Genetic Differences in the Adaptability of Cattle to Tropical and Subtropical Climates***

Experiments were begun in the summer of 1938 to find a practical test that would measure, under field laboratory conditions, the relative efficiency of water expenditure and of heat disposal between genetic types of cattle. These tests consisted in: (1) observing the respiratory rate as an index to the rate of water vaporization through the lungs; (2) determining the transpiration of water through certain areas of the skin as an index to the rate of vaporization of moisture from the skin; (3) determining the nitrogen concentration of the urine as an index to water expenditure through the kidneys; (4) determining the moisture content of the faeces as an index to water expenditure through the excrement; and (5) taking rectal temperatures as an index to efficiency of heat disposal. Tests were made under summer climatic conditions, using pure-bred Aberdeen Angus, half-bred Brahman (zebu) Aberdeen Angus, quarter-bred Brahman × Aberdeen Angus ($\frac{1}{4}$ Brahman, $\frac{3}{4}$ Aberdeen Angus), and pure-bred Brahman cows.

Within each of the four genetic types there is a regular increase in rate of respiration from the lower to the higher shade temperatures. The rate of increase is greatest in the pure-bred Aberdeen Angus and least in the pure-bred Brahman. With the animals held in the sun, the greatest differences are again found within the Aberdeen Angus and three-quarter-bred. Within each of the four genetic types represented there is a regular and significant increase in the amount of water vaporized through the skin as atmospheric temperatures increase. Between genetic types the F values indicate highly significant differences of mean transpiration above 70° F.

The urine concentration of the pure-bred and three-quarter-bred Aberdeen Angus decreases from the cooler to the warmer atmospheric temperatures, whereas with the half-bred and pure-bred Brahman the concentration remains more or less constant at the temperature range recorded.

Between genetic types, insignificant or only slightly significant differences are found in the percentage of moisture in the faeces at each temperature class. On the other hand, highly significant differences are found within each genetic type in the percentage of moisture in the faeces dropped at atmospheric temperatures above 70° F. and below 70° F. class.

As atmospheric temperatures increase above 50° F., and with the animals held in the shade, there is a general and significant increase in rectal temperatures within each genetic type. This is most evident with the pure-bred Aberdeen Angus. With the animals held in the sun, the pure-bred Aberdeen Angus and the three-quarter-bred Angus were significantly influenced, while the half-bred and pure-bred Brahman were not significantly affected by exposure to direct sun rays.

Employing the method described, it has been experimentally determined that the pure-bred and three-quarter-bred Aberdeen Angus are not physiologically adapted to high temperatures and intense solar radiations characteristic of tropical climates. The differences in the physiological response of those and the Brahman cattle to tropical climatic conditions are genetic in origin. The method described may be used in testing parent and progeny strains for inherent adaptability to tropical climatic conditions.

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RHOADES, M.M. ***On the High Mutation Rate of the*** **a**$_1$ ***Allele in Maize Induced by the*** **Dt** ***Gene***

The a_1 allele is the lowest member of a series of four alleles at the A_1 locus in chromosome 3 in maize. Although extensively used in genetic experiments, mutations of a_1 to any of the higher alleles have never been reported. A recently found dominant gene, *Dt*, however, causes a_1 to become extremely unstable. The *Dt* gene is apparently specific in that it affects the mutability of only a_1, there being no effect in the mutation rate of all other tested loci. Mutations of a_1 to the three other members of the allelic series have been obtained, but the frequency with which a_1 mutates to the A_1 and $A^b{}_1$ alleles is a thousand times greater than to the $a^p{}_1$ allele. It is possible that a_1 will mutate to new, previously undescribed alleles. Meagre data indicate that the mutation to the A_1 is more frequent than that to the $A^b{}_1$ allele. Mutations of a_1 have been observed in every part of the plant where this locus is involved in the production of anthocyanins. In the aleurone the number of times a given allele is present may be varied from one to three. When the dosage of the a_1 allele was varied it was found that the frequencies of mutation were in a linear relationship to the dosage of the a_1 allele, i.e. seeds with three a_1 alleles had three times as many mutations as seeds with one a_1 allele, etc. There was a non-linear relationship between the dosage of *Dt* and the frequency of mutation; in seeds with two *Dt*

genes the a_1 allele mutates approximately three times as frequently as in seeds with one *Dt* gene, and in seeds with three *Dt* genes the mutation frequency of a_1 is about eighteen times that in seeds with one *Dt* gene. *Dt* is in chromosome 9, while a_1 is in chromosome 3. Cytological examination at pachytene shows no chromosomal abnormality which can be related to the effect of *Dt* on a_1. Chromosomes 3 carrying an A_1 allele derived by mutation from a_1 are normal in appearance, as are chromosomes 9 in cells in which a mutation to A_1 has occurred. When a mutation of a_1 to A_1 occurs in $a_1\,a_1\,Dt\,Dt$ cells the constitution of the cells following the mutation is $A_1\,a_1\,Dt\,Dt$, i.e. no detectable change has occurred in either of the two *Dt* genes. *Dt* can be regarded as a catalyst since it greatly accelerates the rate of mutation of the a_1 allele but remains unchanged itself when the mutation takes place. The A_1 alleles derived by mutation are stable with either the *Dt* or *dt* alleles. They give the expected linkage with the lg_2 locus in chromosome 3. A dominant modifier *M* has been isolated which inhibits, though not completely, the effect of *Dt* on a_1. A recessive factor has been found which affects the time of mutation. Seeds homozygous for this recessive have much smaller dots of mutant colour in the aleurone, indicating that the time of mutation has been delayed from that commonly observed. Another recessive has been studied which completely inhibits the effect of *Dt*. The mutations of a_1 to the different alleles in the presence of *Dt* are considered as qualitative rather than quantitative changes in the gene molecule, and possibly result from some intragenic reorganization. All available evidence negates the possibility of the mutation of a_1 being due to a position effect. If the *Dt* gene produces some physiological condition in the cell which is conducive to the mutability of a_1, it is possible that the rate at which it elaborates the substance causing this condition might vary at different levels of temperature. Experiments bearing on this point are under way, and the results will be reported at the Edinburgh meeting.

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Riley, H.P. ***Morphogenesis of Flower Parts in* Iris fulva *and* I. hexagona *var.* giganticaerulea**

Differential growth rates in ovaries, sepals, and petals of two species of *Iris* were studied. In the case of each flower part, length and width were plotted logarithmically with width as the *x*-axis and length as the *y*-axis, and the relation between the growth of the two dimensions was expressed by *k* in Huxley's formula $y = bx^k$, in which *b* is the value of *y* when *x* is 1, and *k* is the slope of the line, or the growth coefficient. In a group of clones of *I. hexagona* var. *giganticaerulea* from Barataria, Louisiana, in 1938 *k* was 1·52 for ovaries between 0·4 mm. and about 27·0 mm. in length; just after fertilization, the line shifted and *k* became 0·43 for the growth of the capsule. In 1937, for the same plants, the value of *k* was 1·43 for the ovary before fertilization and 0·55 thereafter. For ovary growth of *I. fulva* from Thibodaux, Louisiana, in 1938 *k* was 1·55 until fertilization and 0·62 after that period, while in 1937, the same clones showed that *k* had a value of 1·89 before and 0·63 after fertilization; another group of clones of the same species from Laplace, Louisiana, in 1937 showed that *k* for ovary growth was 1·48 before fertilization and 0·55 afterwards. When sepals were studied, *giganticaerulea* showed a line with two breaks; for sepals between 4 and 15 mm. long, *k* was 0·92; the claw then began to lengthen at a greater rate than the blade, and the value of *k* for the entire sepal shifted to 1·30; when the flower bud started to open, the blade increased more rapidly in width and *k* became 0·79. For *I. fulva*, only a straight line was found for sepal growth. For plants from Thibodaux, *k* was 1·01 for 1938 and 0·95 for 1937, while plants from Laplace showed a value of 1·00 for *k*. Apparently there is no change in rate of sepal growth at anthesis in this species. For the petals of *giganticaerulea*, *k* was 1·00 until the claw began to elongate, when it became 1·33; after anthesis, the blade grew more rapidly in width and *k* was approximately 0·58. For *I. fulva* from Thibodaux, *k* was 1·25 before and 0·72 after the opening of the flower in 1938 and 1·09 and 0·69 in 1937; the plants from Laplace showed a value of 1·08 for *k* before anthesis and 0·61 afterwards. Regarding sepals and petals, growth in the two species appears to take place at about the same rate during the early stages; when the claw of the sepals and petals of *giganticaerulea* begins to elongate at an increased rate, the rate of the entire structure is changed appreciably. In general, relative growth in *Iris* seems to continue at a definite rate until some event such as fertilization or the opening of the flower occurs; this often changes the growth coefficient.

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Robb, R.C. ***The Relative Frequency of Inheritable Disorders among* 100,000 *Hospitalized Patients***

All the records of the Strong Memorial Hospital, Rochester, N.Y., for ten years past have been reviewed to determine the incidence of genetic defects among persons of all ages and conditions. Although all types of cases are admitted and accommodation is made for self-supporting and indigent alike, this

group cannot be regarded as a random sample of an average New York State population. Rather, it represents that element of the population sufficiently ill, maimed or incompetent to require hospital care. Furthermore, this survey indicates the number presenting symptoms at a specified time, without revealing the proportion who might be similarly affected at a later age. Thus "neoplasia" are reported in about 7 % of these patients, in contrast to the finding of malignancies in 17 % of 3000 autopsied cases.

The most prevalent disorder of presumable genetic etiology is arteriosclerosis, observed in approximately 8000 individuals (but in 11 % of autopsies). The 7600 "tumours" include 1000 fibroma uteri but omit from this category 1600 males with "benign prostatic hypertrophy". Next in order come 3000 hernias (one-quarter umbilical); 1860 haemorrhoids; 1750 diabetics; 1500 with gall bladder disease (two-thirds having stones); extreme obesity in 1400; four kinds of goitre 1300 (one-quarter toxic, eight-ninths of all cases being females); allergy 1300; dementia praecox 1000; cataract 860; varices 700; epilepsy 680; strabismus 610; mental deficiency 600; seventy types of anatomical anomalies 400; myxoedema 366; approximately 200 cases each of glaucoma, congenital heart disease, manic-depressive psychoses, hyperopia and undescended testicles; and fifty other less common conditions to be discussed.

These data will be supported by autopsy statistics, and amplified by a review of the coincidence of these conditions in both of mono- and dizygotic twins.

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ROBERTS, J.A. FRASER. ***Inheritance of Mental Deficiency***

From the practical and administrative point of view mental deficiency is primarily a social conception: the inability of the individual successfully to adapt himself to his environment. It is, however, very closely associated with a measurable characteristic, general intelligence, as determined with so much success upon a scale such as the Binet.

General intelligence, in this sense, is a graded character and displays continuous variation from one extreme to the other. I believe that if we select any human measurement of this kind we can easily perceive certain features which are of fundamental genetic importance. First of all, over the great bulk of the range, there is no discontinuity; we are dealing with the infinitely variable normal differences which distinguish normal people. A frequency curve is found to conform to the normal form. But at the extreme ends of the distribution, most certainly at one end, we find variations which are no longer continuous, and the curve is no longer normal.

Stature provides a convenient example. Over the greater part of the range, in fact over practically all of it, we find the continuous variation of normal people, from the very tall to the very short. But at the lower end of the scale occur the dwarfs, the pathological variants. We find cretins, rachitic dwarfs, midgets, achrondroplastic dwarfs, and others.

General intelligence reveals a similar phenomenon. Without discontinuity anywhere we pass from the brilliant to the superior, the average, the dull, the very backward, and finally to the mentally defective. At the very lowest levels, however, we find not merely the very backward; we find gross deviations, the idiots and the imbeciles, the dwarfs of mentality. As in the case of stature, there is no longer evidence of continuity; this portion of the curve is far from normal, for such individuals are far too numerous.

The distinction, on the basis of measurement only, is not absolute. Both in stature and in intelligence there is doubtless overlapping in this respect, though I believe that when other factors are taken into account and the examination becomes precise the overlapping will be seen to be more a matter of appearance than reality. In any event a broad distinction can be drawn. This distinction is fundamental genetically. As far as determination is genetic—of course this applies to all that follows—we have, on the one hand, multifactor inheritance, on the other, the transmission of single genes; on the one hand, the genes of individually small effect, on the other, the gene whose bearer is sharply distinguished from the rest of his fellows; on the one hand, the host of normal genes, busily engaged in their task of guiding the normal human being along his normal developmental path, and on the other, the single, abnormal gene, rendering normal development impossible, despite the efforts of all the other genes.

It is not impossible to mark approximately the line of division between the two types of mental defective. On the Binet scale it may be drawn roughly at an I.Q. of about 45. Conveniently, this more or less separates those legally classified as feeble-minded, the morons, from the imbeciles and the idiots.

Before considering briefly some genetic aspects of causation in the two groups, let us recall for a moment the very important social distinctions. Feeble-minded persons must be regarded as abnormal, but this is probably true only against the background of our present complex civilization. They are merely the extreme minus end of the normal distribution of intelligence; modern social conditions, however, prove too arduous for the mentally undersized. And the problems they present are serious. Unless cared for and controlled they drift into anti-social activities,

and in the present state of differential fertility in regard to intelligence there is no group in the population which has a higher reproductive rate.

Contrast with this the dwarfs of mental growth, the pathological variants. Their appearance horrifies the unthinking, but they commit no crimes. They are a tragedy and a problem in the lives of the parents to whom they are born, and are far better placed under institutional care. There they absorb the skill and devotion of nurses and attendants. They are a burden to the state, but not an overwhelming one, for amongst children of school age they are not more numerous than, say, 4 in every 1000. They are a group of very low fertility and, actually, most of them are quite incapable of reproduction. Their expectation of life is far lower than the normal. They provide admirable opportunities for scientific observation. The low-grade defective, therefore, may be much the more striking, but as a social problem he is negligible compared to those of high-grade.

The causation of high-grade deficiency is a part of the story of the determination of intellectual level in general. To the extent that general intelligence is genetically determined, and no one can deny that the contribution of heredity is a large one, determination is essentially multi-factor, and the methods to be employed those of biometry. In a social sense these persons may be mentally deficient, but biologically they are the fringe of normality, and properly come within the scope of Prof. Hogben's paper and not mine. I propose to devote the rest of the time, therefore, to the genetics of low-grade mental deficiency.

What are the characteristics of the abnormal genes which are concerned with the determination of low-grade mental deficiency? First of all, they are, in the aggregate, very numerous. There probably exist hundreds of abnormal genes, any one of which can determine, or help to determine, mental deficiency. This proposition is sufficiently obvious, for gross mental deficiency merely implies a grossly imperfect central nervous system, and the causes which can produce this result are as numerous as those which can impair any other bodily system. Where single genes have been identified which are responsible for purely genetically determined mental deficiency, each one is found to be responsible for a small proportion only of the mental deficiency existing in the population. We have only to think of phenylketonuria, infantile amaurotic idiocy, juvenile amaurotic idiocy, or the Laurence-Moon-Biedl syndrome. Probably no one of these accounts for as much as 1 % of low-grade mental deficiency.

From another point of view, the gene which seriously lowers the reproductive rate is necessarily a rare gene. No such gene, that is, a gene which seriously lowers the reproductive rate, has, as far as I know anything approaching the frequency (in the simplex or duplex state, whichever is appropriate) of low-grade mental deficiency.

The second point about these abnormal genes is that the effect upon the central nervous system may not be the only result of their presence. Amongst simply inherited conditions there are epiloia (tuberose sclerosis), phenylketonuria, and the Laurence-Moon-Biedl syndrome, in all of which there are striking effects upon other bodily systems.

We can go much farther than this. It is known that the proportion of mental defectives amongst persons suffering from many simply inherited defects, for example, albinism, is higher, or much higher, than in the general population. Very many of the hundreds of genes which produce human abnormalities cause a gross interference with development, and the result may involve the central nervous system.

The next point is that many of these abnormal genes affect the central nervous system in a proportion of cases only. This is very obviously true in such cases as albinism or Darier's disease, or von Recklinghauser's disease, for the presence of the gene is made manifest by its other effects. Undoubtedly, however, many genes exist which affect the central nervous system in a certain proportion of cases only, but, when the central nervous system escapes, there is then no indication that the gene is present at all. It may well be, however, that very minute examination of the relatives of low-grade mental defectives might sometimes reveal very small signs that they too carry the gene though they have escaped the serious consequences.

The genes of occasional expression, whether they produce other outward effects or not, can of course be regarded as one only of the determining causes of the mental deficiency. But the gene is responsible in the sense that it is an essential factor; but for its presence the individual concerned would have been normal.

Low-grade mental deficiency, then, may be the result of the action of any one of very numerous genes. Few of them, in all probability, are responsible individually for more than, say, 1 % of cases, while many are much rarer than this. A few of them are simple in their action, but most are not. Some may have other effects. And very many of them are genes of occasional expression, producing their effect in some of their bearers only.

Before considering further the nature of the action of these genes, something should be said about other modes of causation of low-grade mental deficiency. Purely non-genetic cases do, of course, occur, but it is probably common ground that they form a comparatively small group. In a genetical review I need not say anything more about them.

What about more complicated genetic schemes, for example, those postulating the co-operation of two or three gene pairs? I think that such causation is likely to be very rare. Even in experimental plants and animals, in instances where there are two contrasted phenotypes only, the pathological variant and the prevalent type, it is very unusual to find two pairs of complementary factors at work.

Simple systems of interaction do sometimes distinguish strains and races of domesticated plants and animals, but we should not be led into drawing too facile an analogy. No doubt the stockbreeder has utilized big, genetically simple variations which have cropped up as the result of mutation; he has artificially fostered their possessors and, by encouraging the rapid accumulation of modifiers, has been able to rob the mutant genes of many of their harmful manifestations, leaving, for the most part, only those which are commercially useful or harmlessly picturesque. But, according to present-day theory, what are of fundamental evolutionary importance are the numerous genes of small effect, no one of which by itself can be very harmful or very beneficial. The startling mutation is of infrequent occurrence, and of minor evolutionary importance, in a species such as man, practising more or less random mating and living in a more or less normal environment.

It seems to me, therefore, that the most probable view is that the genes producing unworkable pathological deviations are by-products of the evolutionary scheme, and that each such gene is likely to exist in rarity and loneliness, the numerous normal genes, and favourable environmental factors, operating against it almost as they would against an external noxious influence.

The abnormal genes may be dominant or recessive. (Sex-linked inheritance I must pass by; of course it can be responsible for a small proportion of cases only.) A number of recessive genes causing mental deficiency are known, and others will doubtless be discovered. It is probable, however, that more cases are due to dominant genes, or to put it more strictly, to genes producing in the heterozygote the effect which we observe, for the excessively rare homozygote might be more severely affected. If such a gene is at all constant in its expression its incidence will not be high in comparison with the mutation rate. Epiloia, as was shown by Gunther and Penrose, provides an example. The majority of these genes, however, produce their effect in a proportion of cases only, it may be in quite a small proportion. All this fits in well with the conception of the greater variability of the heterozygote, an important factor in the mechanism of evolution.

One of the many genes of occasional expression is, of course, one factor only in the causation of a condition. The other factors may be other genes, or non-genetic influences, or both. In the case of mental deficiency the non-genetic factors must necessarily, for the most part, operate before birth.

I have given a few of the reasons for supposing that one or two other gene pairs will very seldom provide the additional genetic factors. When these factors are genetic they are likely to be the numerous normal genes of small effect. They might be genes which determine the level of general intelligence in the normal population, or they might be modifying genes not having this separate effect.

An important genetic point arises here. There is possibly a connexion between high- and low-grade mental deficiency. Penrose has suggested, and produced good evidence to demonstrate the point, that sometimes the relatively high-grade mental defective might be the heterozygote, while the gross idiot is the homozygote. While fully accepting this view, I think it is likely that there is a commoner association. A gene determining low-grade mental deficiency may well be more frequently expressed in persons very low in the scale of mentality. In other words, a concentration of genes producing a somewhat extreme modification may be a favourable background from the expression of an abnormal gene producing a much more extreme modification in the same direction.

The other necessary condition for the appearance of low-grade mental deficiency will often be, or usually be, pre-natal non-genetic factors. Can we hazard a guess as to their mode of action, for actual knowledge is scanty? A consideration of those conditions whose frequency increases with advancing maternal age is a helpful example in this connexion. Mongolism is the most notable case. This condition exhibits a familial incidence, definite though small, and it may be that underlying mongolism as one of the essential factors in its causation is a gene of very low frequency of expression. A number of other abnormalities too become commoner as maternal age advances.

Is it possible that this phenomenon, and other similar ones, provides a clue? Laboratory experiments on the effect of parental age yield almost negative results when large numbers are studied. May it not be that the effect of many abnormal genes is to make the developing embryo unduly sensitive to slight variations which would be of no consequence to the normal foetus? Perhaps the margin of safety is reduced, so that the embryo, bearing the single, abnormal, mutant gene, instead of being robustly protected against anything less than a major disaster, pursues its development, or parts of its development, upon the edge of catastrophe; whether catastrophe actually supervenes or is avoided then depends upon the most trivial circumstances.

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ROBERTS, J.A. FRASER. ***Resemblances in Intelligence between Sibs Selected from a Complete Sample of an Urban Population***

The attempt was made to secure a complete sample of children of school age, a cross-section of the population, by ascertaining and giving a mental test to all the children living within a defined area on a given date and whose dates of birth fell within certain limits. It is believed that the group, 3400 children, is practically complete. Various observations and measurements have been carried out on these children and on various subgroups. In particular, detailed family and social investigations have been made on three special groups, composed respectively of the brightest 4 %, the median 4 % and the dullest 8 %. All the sibs of school age of these children also received a mental test. The deviation from the mean of the sibs of children of the two extreme groups is rather more than 0·6 of the mean deviation of the children themselves. The whole group of 3400 yielded a number of sets of sibs, equivalent to a comparison of about 650 pairs. The sib-sib correlation coefficient was 0·534. The findings closely resemble those to be expected in the case of a graded character very largely determined by multi-factor inheritance. The resemblance between sibs appears to be at least as great as is found in the case of any physical characteristic.

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ROBERTSON, D.W. ***Studies of Barley Genetics in Colorado***

Barley genetics studies have been conducted at the Colorado Experiment Station, Fort Collins, for the past 14 years. At various times data have been published on the linkage relations and interaction of the various factor pairs studied. Under normal climatic conditions genetic differences such as red pigmentation of the veins on the lemma, straw colour, and chlorophyll deficiencies are very easily distinguished. This makes it rather convenient to study them in the field. Chlorophyll deficiencies are picked up quite frequently under field conditions. The station is located at about 5000 ft. above sea-level. From these studies the following factor pairs have been placed in seven linkage groups:

Group I contains the factor pairs (**Vv**) two-row versus six-row, (**Ff**) green versus chlorina in Minn. 84–7, (**Pr pr**) purple versus non-purple straw, (**Or or**) green versus orange seedling in Trebi IV, and (**Yy**) green versus virescent seedlings in Minnesota 72–8.

Group II contains black versus white lemma (**Bb**) and ($A_t a_t$) for green versus white seedlings in Trebi I.

In Group III the following factor pairs have been located: Covered versus naked caryopsis (**Nn**) and green versus white seedling ($A_{c_2} a_{c_2}$) in Coast II.

Group IV contains the following factor pairs (**Kk**) for hoods versus awns; (**Ii**) for intermediate versus non-intermediate, and (**Bl bl**) for blue versus non-blue aleurone.

Group V contains the factor pairs (**Rr**) for rough versus smooth awn, (**Ss**) for long- versus short-haired rachilla, and one of the factor pairs for branched versus unbranched stigma (**Uu**) Another factor pair for green versus white seedling has also been placed in this group ($A_b a_b$).

Group VI contains four chlorophyll-deficient seedlings arranged in the following order on the chromosome: ($A_c a_c$), ($X_c x_c$), ($A_n a_n$), and ($X_s x_s$). The ($A_c a_c$) factor produces green versus white seedlings in Colsess I, ($X_c x_c$) green versus xantha seedlings in Colsess IV, ($A_n a_n$) green versus white seedlings in Nigrinudum I, and ($X_s X_s$) green versus yellow seedlings in Smyrna I. In studies made to determine the effect of several factor pairs in the heterozygous condition on growth, no detrimental effect was found when plants carried either the factor pair ($X_c x_c$) or ($A_c a_c$) in the heterozygous condition. However, when both factor pairs were carried in the heterozygous condition in the same plant, an increased grain yield was obtained over pure green plants or over plants carrying other lethal genes in the heterozygous condition, indicating the possibility of dominant growth factors being carried in the end of the chromosome marked by the ($X_c x_c$) ($A_c a_c$) factor pairs.

Group VII contains the factor pairs ($F_c f_c$) for green versus chlorina seedling found in Colsess V and ($Y_c y_c$) for green versus virescent seedlings in Coast III.

Another factor pair ($f_{c_2} f_{c_2}$) for chlorina seedlings found in Coast V was found to be inherited maternally. When Coast V was used as the female parent, all of the progeny were chlorina (pale green). When Coast V was used as the male parent in crosses with normal green plants, all of the progeny were normal green. Factor pairs located in the seven linkage groups segregated independently of the female plant colour.

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RUSSELL, W. LAWSON. ***Physiological Genetics of Guinea-pig Coat Colour***

In an attempt to elucidate some of the processes by which colour genes produce their effects the following results were obtained:

(1) Natural pigmentation in the epidermis is similar to that, observed by Wright, in the eye, both in its quality and in the order of effect of the genes studied.

(2) The technique used in treating frozen sections of skin with a buffered solution of dopa produced adequately uniform results within each genotype.

(3) The effect of gene **s** was shown by the absence of any dopa reaction in the white area of a white-spotted animal that gave a full reaction in the black area. Combinations with **e e** gave, in the hair bulbs, slightly, but significantly, less reaction than the corresponding combinations with **E** –, while there was no difference between the reactions in the basal layer of these two combinations. As far as the evidence goes there was no difference in reaction between the two phases of colour production found in agouti, **A**–, and the reaction obtained agreed with that found in **a a**. As compared to a strong reaction with **C** – the lower alleles of the albino series gave no reaction in the basal layer and reduced reaction, or no reaction, in the hair bulbs. In the hair bulbs four significantly different levels of reaction were shown: none with $c^{r\,or\,a}c^{r\,or\,a}$ combinations, weak with $c^{k\,or\,d}c^{r\,or\,a}$, medium with $c^{k\,or\,d}c^{k\,or\,d}$ and strong with **C** –. Combinations with **f f**, as compared with **F** –, gave no difference in reaction in the basal layer, but significantly less reaction in the hair bulbs. Combinations with **p p** showed almost no reaction in the basal layer, while the hair bulbs gave as strong a reaction as those in the corresponding **P** – combinations. If the gene **b** had any effect in the few combinations in which it was tested, it can only have been a slight reduction.

The following physiological genetic interpretations are made:

(1) Gene replacements at the **C** and **F** loci alter the amount of natural yellow pigment produced in the hair by affecting the concentration or activity of the enzyme system present.

(2) In the epidermis the lower alleles of the **C** – series and **p** produce their effects, at least in part, by reducing the concentration or activity of the enzyme system present.

(3) There is a difference in the enzyme systems active in pigmentation in the two locations, skin and hair.

(4) There is a failure of enzyme in the white areas of **ss** animals.

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SAEZ, A. ***Efectos de la centrifugación sobre las células sexuales de*** **Schistocerca paranensis**

Con el fin de estudiar los efectos de la centrifugación sobre las células sexuales teniendo en cuenta especialmente los diferentes estadios del período meiótico, el autor realizó una serie de experiencias tomando como material el ortóptero *Schistocerca paranensis* por ser este bien conocido desde el punto de vista de su citología normal. Se han sometido animales enteros y vivos a la acción de la fuerza centrífuga habiéndose comprobado que el mismo animal mantiene las condiciones fisiológicas requeridas para que las células se hallen en un medio adecuado y natural.

Se realizaron diversos esperimentos sometiendo los individuos a 4000 y 5000 revoluciones por minuto, o sea teniendo en cuenta el diámetro de la centrífuga respectivamente a 2000 y 3000 veces la fuerza de la gravedad.

Se sometieron a diferentes tiempos que variaron de 15 minutos a 2 horas. Las células manifiestan en diverso grado la influencia de la fuerza centrifuga observándose la estratificación de los distintos componentes del sistema celular de acuerdo a su gravedad específica relativa o sea el desplazamiento de los mismos según su mayor o menor peso específico.

Se ha constatado que los distintos estadios del período meiótico son influenciados de modo diferente. Los estadios mas sensibles son los leptoténicos y tambien las metafases goniales y meióticas, así como las fases que preceden a éstas y los estados finales, tales como anafases y en general los estados en que la cromatina se halla en estado de máxima condensación.

En las diacinesis los cromosomas se orientan polarizando sus extremos hacia el polo centrífugo. Lo mismo respecto al cromosoma sexual que tiene menor peso especifico durante la metafase spermatogonial que los demás autosomas.

El nucleolo se estratifica en menor grado que el cromosoma sexual durante los estados paquiténicos y en las espermátidas. Se han observado tambien rotaciones en senti do centrípeto de algunos núcleos mientras que sus componentes se hallan orientados y desplazados hacia el polo centrífugo de la célula.

Es indudable que la centrifugación produce cambios durante las diversas etapas de la meiósis y es muy probable que dichos desplazamientos induzcan la produción de mutaciones cromosómicas de diverso grado e intensidad.

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SALAMAN, R.N. ***Breeding for Immunity to Blight and other Diseases in the Potato***

Blight (*Phytophthora infestans*) broke out in epidemic form in Europe in 1845, followed by a similarly devastating attack in 1846. Since then it has been endemic with frequent epidemic exacerbations.

No domestic variety growing in 1845 showed any resistance to the new disease. In subsequent years new varieties, such as Champion, Sutton's Flourball and Magnum Bonum, were acclaimed as highly resistant: and indeed in their early years they do appear to have

shown some resistance, which completely disappeared later.

Research at the Potato Virus Research Station, Cambridge, has shown that not a single domestic variety, including those mentioned above, shows the least resistance to common blight when tested in the laboratory.

In 1851 Goodrich introduced a Peruvian variety with the view of combating blight: from this he bred certain well-known varieties; none, however, displayed the desired quality. We now know that Goodrich's variety was one of the Andigenum group, in which, as we have shown at Cambridge, there is no inherent genetic basis of resistance.

In 1908, R. N. Salaman discovered a true genetic resistance to *Phytophthora* independent of maturity, in the selfed seedlings of *S. edinense*. Hybridization with these resistant forms was carried on, and it was found that after three years many of the originally resistant seedlings and their hybrids succumbed to blight in the open. One seedling, however, was maintained in the garden without ever being lifted during the winter for 17 years; it never exhibited a trace of blight. The reason for this was not discovered till a few years ago.

In 1914, R. N. Salaman disovered that *S. utile*, better known as *S. demissum*, showed an outstanding immunity to *Phytophthora infestans*. Hybrids were made with domestic varieties, some of which showed resistance in the field. The work was resumed with further interspecific hybridization in 1922. Varieties derived from these *S. demissum* crosses by selfing and backcrossing are with us to-day and combine good economic characters with complete resistance to the *common form* of *Phytophthora infestans*.

In 1928, Salaman introduced a simplified laboratory method of testing very young seedlings in such a manner that many thousands could be tested in a season. Later, leaves only were used for testing, which facilitated the work. Pettersson at Cambridge has somewhat modified this method, making it more reliable and more rapid.

Miss O'Connor, working at Cambridge, discovered that this new infection was due to a biotype of the fungus, which has since been isolated in single-spore cultures by Pettersson. In Germany the same was discovered, and intensive research there has resulted in the discovery of more biotypes. Miss O'Connor, however, found in the Cambridge collection a South American species resistant both to the common and to the new form of *Phytophthora infestans*. Subsequent research has shown that this second genetic resistance exists in certain types of *S. demissum* and allied species from Mexico.

We have now built up new varieties in which both types of resistance are present together with some of the desirable economic qualities of our domestic varieties. These "double resisters" have not yet the economic status of our "single resisters", but there is no reason why such should not be attained with further breeding.

All our resistant plants are bred for resistance to wart, and an effort is being made—at present with but scant success—to include in their composition resistance or tolerance to the major virus diseases.

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SANDERS, J. *A Family with Pick's Disease*

In 1896 Pick described a syndrom, characterized by special, serious disorders of speech and a fast-developing decay and atrophy of the temporal lobes of the brain. This disease was in the following years the object of much research both clinical as well as anatomical.

My colleague Schenk of the asylum Oud-Rosenburg in The Hague and I have examined a family of which sixteen persons suffer, or have suffered, from Pick's disease. This is the largest family, thus affected, mentioned till now. Grunthal in 1930 described two brothers, who both grew ill with Pick's disease in the same way. In 1931 he published a report of two sisters and the son of one of them; and Braunmuhl and Leonhard also of two sisters, all suffering from this disease. Kufs and Reich, and also Schmitz and Meyer, described in 1933 a family of which three sisters and their father, as well as his brother, had Pick's disease.

The disease begins at the age of about 40–50 years and may last for 10 years. The patient becomes childish and gradually demented. He repeats several times the few words he can say and makes rhythmic movements.

We have examined all patients with the Rorschach test and the National intelligence test. For the Rorschach test ten cards with ink-blots are shown to the patient. He must tell us what figures he sees in these blots, viz. clouds, animals. Not only the patients, but all members of the family were examined. Some persons gave very strange answers, though the family had not yet noticed any psychical changes. But 1½ years later we were informed that three persons had gradually changed psychically and the diagnosis of Pick's disease was very easily made.

There are other members of this family, who are now 25–35 years, and who we expect will suffer from Pick's disease when they reach an age of about 45 years. We have come to this conclusion from their behaviour and the result of the Rorschach test.

It is very important from a eugenical point of view to recognize as soon as possible those who are predisposed to the disease. If it were possible to

recognize them before their marriage it should be possible to stamp out the disease, since it is caused by a dominant gene.

We cannot prove yet that our theory is true; the future will show. But in three cases our supposition is already confirmed.

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SANSOME, E.R. ***Abnormal Meiosis in* Pisum sativum**

Two sister plants from an F_2 family showed a variable proportion of bivalents at metaphase of meiosis. The number of bivalents per nucleus ranged from 0 to 7 with a maximum number of nuclei having 4 bivalents. An analysis of chiasma frequencies shows that the chiasma frequency per actual bivalent is only slightly lower than that of normal plants. There is no correlation between chiasma frequency per actual bivalent and number of bivalents per nucleus. Univalent formation, in this case, therefore, does not appear to be due to an interference with the amount of pachytene pairing, but, rather, to some reaction of a "trigger" nature inhibiting chiasma formation.

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SCHADE, H. ***Beitrag zur Feststellung der Häufigkeit von Erbkrankheiten***

Voraussetzung für praktische Rassenpflege ist die möglichst genaue und vollständige Erfassung aller erbbedingten Eigenschaften. Eine erbbiologische Bestandsaufnahme, wie wir sie durch Untersuchung von über 4000 Personen einer alteingesessenen bäuerlichen Bevölkerung in der Schwalm durchgeführt haben, soll unter Berücksichtigung des genealogischen Aufbaues und der Bevölkerungsbewegung Aufschluss geben über alle gesunden und krankhaften, körperlichen und geistigen Eigenschaften der Bevölkerung und die Verbreitung ihrer Erbanlagen. Dazu gehört auch die Häufigkeit der Feststellung von Erbkrankheiten. Solche Häufigkeitsfeststellungen sind bisher in Wohnbevölkerungen nur wenige und zwar meist auf Grund von Zählungen getroffen worden.

In unserem Material fanden sich:

Sympt. Psychosen: 4 = 1·0 °/₀₀.

Schizophrenie: 10 = 2·5 °/₀₀ (ausserdem fraglich 2 = 0·5 °/₀₀).

Man. Depr. Irresein: 2 = 0·5 °/₀₀ und 2 = 0·5 °/₀₀ Cycloide (ausserdem fraglich 3 = 0·75 °/₀₀).

Genuine Epilepsie: 14 = 3·5 °/₀₀. Sympt. Epilepsie: 5 = 1·25 °/₀₀.

Schwachsinn: 35 °/₀₀ (davon schwere Formen 5·0 °/₀₀).

Über die Häufigkeit angeborener körperlicher Missbildungen in geschlossenen Bevölkerungen ist bisher nichts eingehendes bekannt. Es liegen lediglich Untersuchungen über einzelne Missbildungen in bestimmten Bezirken vor. Es fanden sich in unserer Bevölkerungsgruppe:

Angeborene Hüftverrenkung: 2·5 °/₀₀.

Klumpfuss: 2·5 °/₀₀.

Lippen-Gaumensplate: 2·25 °/₀₀ (davon nur Hasenscharte 4 = 1 °/₀₀).

Die Häufigkeit der angeborenen körperlichen Missbildungen insgesamt beträgt in unserer Bevölkerung etwa 1 %.

Der Versuch, die Häufigkeit innerer Krankheiten in einer Wohnbevölkerung zu bestimmen, ist bisher noch nicht unternommen worden. Auch die inneren Krankheiten beruhen ja auf dem Wechselspiel zwischen erblichen Veranlagungen und den Einwirkungen der Umwelt. Zum Beweis der Erblichkeit auch innerer Erkrankungen sind auffallende Befunde mit Häufung dieser Leiden in bestimmten Familien wiederholt veröffentlicht. Erst dann aber, wenn man weiss mit welcher Wahrscheinlichkeit solche Häufungen in der Familie allein nachdem Zufall gefunden werden, kann man sagen welchen Anteil die erbliche Disposition hat. Solche Berechnung lässt sich aber erst anstellen auf Grund von Zahlen, die die Häufigkeit der einzelnen Erkrankung in einer Bevölkerung belegen.

Es wurden die Häufigkeiten für mehrere Krankheiten berechnet. So wurden, z.B., Ulcus ventrikuli- und duodeni-Kranke 10·2 a.T., Diabetes mellitus bei 2·5 a.T. gefunden. Diese Ziffern sind Mindestzahlen, da es zum Zeitpunkt der Untersuchung oft nicht mehr sicher festzustellen ist, ob, z.B., sicher ein Ulcus ventrikuli vorgelegen hat und Röntgenbefunde in einer bäuerlichen Bevölkerung oft nicht vorliegen. So ist die Diagnose auf ausgeheiltes Ulcus in weiteren 2·25 °/₀₀ mit grösster Wahrscheinlichkeit, aber nicht mit Sicherheit zu stellen.

Es erscheint wünschenswert, dass Vergleichsstatistiken aus anderen Bevölkerungsgruppen erarbeitet werden.

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SCHOENHEIMER, S. GLUECKSOHN-. ***On a New Short-tail Mutation in Mice***

The new dominant short-tail mutation **Sd**, which originated in Danforth's laboratory and was reported by Dunn and Gluecksohn-Schoenheimer (1938), was found to have a strong effect on the urogenital system and the intestinal tract as well as on the tail.

Animals heterozygous for **Sd**, all of which are

either tailless or have a short tail up to about one-third normal, show malformations of the kidneys and ureters (111 newborns examined). These structures may be missing entirely or be hypoplastic, or one kidney and ureter may be missing while the others are normal or hypoplastic. Sometimes both kidneys are missing while both ureters are present. The viability of the affected animals is greatly reduced. Animals with extreme defects fail to survive. Dissection of sixty-three normal litter-mates showed their urogenital systems to be entirely normal.

The homozygotes are entirely tailless, have no anal opening, and either a very small or no genital papilla; they have a marked lesion in the sacral region (spina bifida) (Dunn and Gluecksohn-Schoenheimer, 1938). At dissection these animals were found never to have any kidneys (twenty-eight newborns dissected). Their ureters very often are entirely missing; if present they are reduced in length and displaced. The bladder and the urethra may be present or missing. With the atresia of the anus there is associated an atresia of the rectum and sometimes of part of the colon. The animals have a persistent cloaca; rectum, urinary and genital ducts join a common sinus. As in similar malformations known in humans the morphology of the structures affected in these mice shows great variability. The lesion in the sacral region is always found associated with a ventral or dorsal spinal cyst. These animals die within 24 hr. after birth.

The embryonic development of these malformations is being studied.

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SCHREIBER, F. ***The Genetics of Partial Coloration in Beans*** **(Phaseolus vulgaris)**

Since the discovery of the Mendelian laws, many geneticists have been engaged in finding out the inheritance of the seed-coat pattern of the garden bean. It was so complicated that H. N. Kooiman wrote in 1931 in his *Genetic Monograph on "Phaseolus"*: "A factorial scheme that is generally applicable cannot with any degree of reliability be furnished." R. A. Emerson found out that the dominant factor **P** must be present for the development of any coloration in the seed coat of beans, and the recessive factor **t** for partial coloration, dominant **T** being responsible for total pigmentation. Among the partial coloured beans **PPtt**, there are types with more or less coloration, for the degree of colour extension of which Tschermak made the factor allelomorphs **Z–z** responsible.

In 1934 I found that a fourth factor **L** exists, which is able to limit or reduce the partially coloured area of the bean coat. Further research work led to the conclusion that the main types of partially coloured beans are due to the interaction of the two genes **Z** and **L**. There is a considerable incomplete dominance between the two, with one exception only, so that we get seven different F_2 phenotypes after the cross **PPttZZll** × **PPttzzLL**. The F_2 phenotypical ratio is as follows:

ZZLL 1, Marginata type, white seed coat with hilum margin.
ZZLl 2, Ambigua type A, medium coloured area.
ZZll 1, Expansa type, large coloured area.
ZzLL 2, Laciniata type, white with coloured caruncula.
ZzLl 4, Intermedia type, coloured eye with margin.
Zzll 2, Ambigua type B, medium coloured area.
zzLL 1, Erasa type, homozygotic, white.
zzLl 2, Erasa type heterozygotic, white.
zzll 1, Restricta type, small coloured area, eye.

The two Ambigua types and the two Erasa types cannot be phenotypically distinguished so that we have to count them together. Therefore we get the segregation ratio 1 Marginata : 4 Ambigua : 1 Expansa : 2 Laciniata : 4 Intermedia : 3 Erasa : 1 Restricta. Four of these types are homozygotic, the others heterozygotic segregating according to the above formulae.

A problem which has presented much difficulty during recent years is thus solved. A multiplicity of segregating types can be caused by incomplete dominance of only a few genes. It is to be supposed that similar conditions may underlie the inheritance of physiological phenomena.

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SCHREIBER, G. ***Alcuni aspetti genetici del problema della metamorfosi degli anfibi***

Nello studio della metamorfosi degli anfibi apparisce il concorso di due fattori nettamente distinti: uno, l' azione ormonica tiroidea, l' altro, la costituzione genetica degli abbozzi degli organi metamorfosanti.

In alcuni casi speciali che ho studiato precedentemente, questi due fattori della metamorfosi si manifestano molto chiaramente. Questi casi sono: (*a*) la neotenia degli Urodeli, e particolarmente del Proteo, dove l' indipendenza della funzionalità tireo-ipofisaria rispetto alla reattività tissulare appare evidente; (*b*) la metamorfosi accelerata da tiroide dei girini di anuro e le disarmonie che appariscono in conseguenza.

Un terzo caso, nel quale la costituzione genetica potrebbe presentarsi particolarmente interessante, è tutt' ora in via di studio ed è la ricerca statistica di

una popolazione di girini in metamorfosi nati da un unica deposizione.

Nel *Proteus* ed in alcune specie affini, non si è mai riusciti ad ottenere la metamorfosi con somministrazione di ormoni tiroidei e ipofisari, mentre è dimostrata la perfetta funzionalità del sistema endocrino di questi animali. La mancanza della metamorfosi si deve quindi riportare ad una deficenza della reattività dei tessuti.

In varie esperienze, mediante trapianti, ho potuto dimostrare l' indipendenza tra la reattività dei tessuti e la funzione endocrina.

Infatti la pelle di Proteo trapiantata su Axolotl non metamorofosa quando l' ospite viene fatto metamorfosare con iniezioni di tiroxina.

D' altro lato trapianti in senso inverso, di pelle di Axolotl su Proteo successivamente iniettato con tiroxina, hanno mostrato la perfetta metamorfosi del lembo di pelle di Axolotl innestato. La tiroxina può quindi circolare indisturbata nel corpo dell' urodelo neotenico e agire sui tessuti della specie ad essa sensibile.

Il comportamento così diverso dei tessuti omologi di specie di Urodeli deve quindi risiedere nella natura genetica specifica del tessuto e non nelle condizioni ormoniche dell' ambiente.

La nozione di recettività locale specifica verso un ormone, legata alla costituzione genetica della specie, apparisce ancora più complesso nelle esperienze sugli Anuri.

In queste esperienze ancora un altro fattore, molto probabilmente legato alla costituzione genetica della specie, entra in giuoco, cioè la velocità di accrescimento dell' organo endocrino e della sua funzione.

Ho denominato "serie moforgenetica" la serie degli episodi metamorfici legati al progressivo accrescimento funzionale di una ghiandola endocrina e quindi alle concentrazioni minime efficaci di ormone successivamente verificantesi nell' ambiente interno.

Una immediata applicazione di questo concetto si trova nella interpretazione delle disarmonie dei girini fortemente tiroidizzati.

In questi casi, fin dall' inizio della tiroidizzazione, si ha una concentrazione ormonica superiore a tutti i minimi efficaci corrispondenti ai vari episodi e i vari abbozzi iniziano quindi la loro metamorfosi contemporaneamente; non essendo così seriati cronologicamente come nella metamorfosi normale, essi non hanno il tempo necessario a completare le loro modificazioni specifiche ed il loro accrescimento volumetrico.

Nella metamorfosi, gli abbozzi a sviluppo più lento sono quelli che nelle esperienze colla tiroxina reagiscono a dosi inferiori. Ciò ci permette di dedurre che nella metamorfosi normale il progressivo aumento di funzionalità dell' organo endocrino comanda, col meccanismo delle soglie di azione, l' inizio delle modificazioni metamorfiche prima agli organi a sviluppo più lento e successivamente agli altri. Così gli organi a lento sviluppo hanno il tempo necessario al loro completamento e l' organismo si sviluppa in modo perfettamente armonico.

La velocità di sviluppo della ghiandola endocrina deve quindi essere considerata come un carattere specifico legato alla costituzione genetica e le sue alterazioni sperimentali portano come si è visto allo sviluppo disarmonico.

D' altro canto la recettività degli organi è pure un carattere specifico e independente da quello della funzionalità tiroidea.

Si possono quindi prospettare ulteriori ricerche sul comportamento di tali caratteri e sulle modificazioni del processo metamorfico legate alla trasmissione ereditaria di essi negli incroci tra specie a differente velocità di metamorfosi.

Così pure possiamo pensare che i trapianti reciproci di ghiandole endocrine tra queste varie specie possano portare a fenomeni di disarmonia analoghi a quelli sopra descritti nelle esperienze di tiroidizzazione.

Studiando statisticamente il decorso della metamorfosi in una popolazione di girini derivati da una deposizione unica, si possono mettere in evidenza variazioni del processo metamorfico dipendenti da fattori ambientali e da fattori genetici.

In una ricerca preliminare sono stati considerati otto stadi tipici della metamorfosi del Bufo, scelti in modo da poter venire rapidamente e sicuramente riconosciuti per mezzo di particolari anatomici visibili ad occhio nudo. In una deposizione di un migliaio di girini è stato ad intervalli di tempo regolari contato il numero di quelli che avevano raggiunto i vari stadi, costruendo così delle curve di sopravvivenza dei vari stadi.

Poiche le curve mostrano la velocità del processo metamorfico e la durata degli intervalli tra i vari stadi, si possono analizzare le condizioni ambientali o genetiche che incidono su tale velocità. Queste curve ci offrono quindi un rivelatore della velocità di sviluppo della tiroide come carattere ereditario e d' altro canto possono servire come rivelatori di condizioni sperimentali agenti su di essa o agenti direttamente sui fenomeni morfogenetici dei singoli organi nei casi della tiroidizzazione sperimentale.

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SCHULTZ, J. ***The Function of Heterochromatin***

The chromocentres of the resting nuclei were shown by Heitz to have their origin in special regions of the chromosomes, characterized then as heterochromatic because of this property of persisting as dense and

compact bodies. There are many chromocentres in a nucleus, but they are most evident at the spindle attachment and at the ends of the chromosomes. As the nuclei grow—see, for example, the account of Painter and Griffin (*Simulium*) and that of Frolowa concerning the nuclei in the *Drosophila* larvae—the chromocentre grows into a mass of chromomeres which, instead of pairing regularly as the other regions of the chromosomes do, appear coalesced into a common mass. This coalescence persists when large portions of the heterochromatic regions are removed from their normal position in translocations. The simplest interpretation of the facts is then that these are regions of the chromosome having the property of non-homologous association. Since the chromocentres are formed at telophase, this type of association must occur at that time, and observation of the anaphases of such translocations indicates that it may begin even earlier, suggesting a relation of the heterochromatic regions to the spindle attachments themselves.

Not all heterochromatic regions appear to have the property of non-homologous association—for example, the situation in some of the Chironomids as described by Bauer. Whether this difference is a difference in the pattern of mitosis, or in the nature of the heterochromatin, is difficult to say. Thus, while in some species the non-homologous association is characteristic of heterochromatin, in others it is not.

In the Chironomids Bauer has defined the heterochromomere as consisting of a capsule with an achromatic centre and a deeply staining cortex. Similar structures occur in *Drosophila* also, and, in spite of the considerable variability of the chromocentre, it would appear that for this kind of heterochromatin, heterochromomeres are the basic structures. At the ends of the chromosomes, however, the non-specific associations that occur---examples are numerous, not only in the salivary gland chromosomes—do not appear to be correlated with the formation of heterochromomeres. The two different criteria, the heterochromomere and the non-specific association, do not appear at first glance to be correlated. It is, however, possible that they represent the opposite extremes of a process related to another property of the heterochromatic regions, namely, the formation of nucleoli. The satellite chromosomes of Heitz are cases in point, and so also is the nucleolar organizer of *Zea mays*. In maize, McClintock's demonstration that in the absence of the nucleolar organizer other regions form nucleolar blebs may be taken to indicate that all regions contribute to the formation of the nucleolus.

The nucleolar regions in the salivary glands of the Diptera are quite analogous to those mentioned, and derive from heterochromatin. The great size of the chromosomes, however, show formations in the other regions of the chromosomes (neben-nucleoli in the Chironomids—Bauer, Poulson and Metz; puffs in *Drosophila* and *Sciara*—Bridges, Poulson and Metz) which are entirely comparable to the formations in *Zea*. Thus the ability to form nucleoli is not restricted to the major heterochromatic regions but is found in a whole minor group as well.

The cytological peculiarities of the heterochromatic regions affect both the nucleic acid and the protein—the staining and the non-staining portion of the chromosomes. It should be remembered that these characteristics are variable, and that the various nuclei in a single organism behave differently. For example, the sex chromosomes are usually completely heterochromatic during spermatogenesis; but they are not heteropycnotic during oogenesis. Or in the salivary gland of a male, the *X*-chromosome is broader and fainter than the comparable female *X* haploid strand. These variabilities call for caution in interpretation without further evidence from the genetical analysis.

It is to be remembered that the genetical method of analysis involves the study of differences, and that it is therefore at its weakest when dealing with functions for which there is a considerable "margin of safety". The analysis of the metaphase chromosome maps in *Drosophila melanogaster* showed that relatively few genes are located in the heterochromatic regions in proportion to a comparable length of "euchromatin" (Muller and Painter, Dobzhansky, Heitz). The conclusion was at first drawn that the great bulk of the region was due to inactive genes (Muller and Painter, Heitz), and later, as the result of translocation studies within the heterochromatin of the *X*, that relatively few genes were present which produced accessory substances at mitosis, hence the great size.

There have been a few mutants located in these regions, both genetically and cytologically. They have no especially distinctive phenotype---cubitus interruptus, bent, light, bobbed, straw; an eye colour; a venation character, and so on. The genes controlling the size of the heterochromatic region of the *X* at metaphase have been located in a few bands of the salivary gland chromosomes (Muller, Raffel, Gershenson and Prokofyeva-Belgovskaia). The locus appears to be the same as that of the nucleolar organizer (Schultz and Catcheside, Kaufmann). According to the work of Neuhaus the situation in the *Y*-chromosome may be similar, with the large metaphase block proximal to the spindle attachment. Thus the evidence from gene localization is consistent with the view that the heterochromatic regions consist of only a few genes.

The evidence from dosage experiments may be interpreted similarly. Duplications or deficiencies of the *Y*-chromosome have little effect on viability, cell size, or any of the obvious morphological characters of the organism. The most striking effect is on the

motility of the sperm in the male; the *XO* male, and males deficient for various parts of the *Y*, are sterile (Bridges, Stern). Not only a deficiency but also an excess of *Y*-chromosomes has this effect: the *XYYY* male in *D. melanogaster* is sterile also. This means that the effect of the *Y* on spermatogenesis, like most gene effects, is the result of a balance involving genes outside the *Y* as well. The balance is different in different species—in *D. virilis* the *XYYY* male is fertile, while in *pseudoobscura* there is evidence indicating that the situation is like that in *melanogaster*.

There are now data from another type of experiment. The position effects—using the term loosely—at the loci of chromosome rearrangements in the heterochromatic regions have given another mode of attack. For the male sterility effects resembling those found in the dosage experiments occur in *Y* translocations, although it cannot be said that the situation is clear as yet, despite the extensive and thorough work of Neuhaus. The other genes located within heterochromatic regions give typical cases of position effect —one need only mention cubitus interruptus, for example. The striking effects in such rearrangements are not on the genes in the heterochromatin but rather on those juxtaposed to the heterochromatic regions as a result of the translocation. The majority of the eversporting types of Muller, with their characteristic mosaicism or variegation, belong to this group of translocations. Since most of these translocations have been detected as variegated mutants in X-ray experiments, they are a selected group. However, tests made both by myself and by Noujdin have shown that the same phenomenon occurs in a less selected group of rearrangements involving heterochromatic regions. I shall limit myself here to a brief description, indicating the basis of the general rules that have been applied (Schultz).

Conclusions about the cell lineage and the developmental relations of the changed cells can be drawn from the pattern of variegation. This has the limitation that comparable tissues must be used and the effects of the genes to be studied must be visible in all of them. In the cases under discussion the variegation concerns mostly the genes around the white and the yellow regions in the *X*-chromosome and the brown and light regions of the second. There are a few cases in other regions, and it seems likely that adequate test will reveal the presence of the phenomenon in many more.

A representative case is the *X* 4 translocation, w^{vD^3}, kindly sent to me by Dr M. Demerec. The break in the *X*-chromosome is between diminutive and echinus, and that in the fourth is at the locus of cubitus interruptus. At a temperature of 25°, females heterozygous for this translocation, tested with the genes from the tip of the *X* to the point of rearrangement, show slight variegation for split and extreme variegation for diminutive. They also show a slight Minute variegation which can be ascribed to a locus in the *X* to the right of the break. There may also occasionally be a slight Notch effect. At 16° (intermediate temperatures are intermediate) variegation for the white locus is manifest, it is extreme for Notch, and the whole fly is now diminutive except for the ovary. Such flies are fertile even though diminutive is female sterile. The nature of the variegation for the white locus also varies with temperature: when the variegation is extreme, most of the eye has the colour of one of the very pale allelomorphs, ecru or tinged, and the spots are cherry. At intermediate temperatures the ground colour becomes darker, close to apricot or cherry, the spots now being more like the colour coral. Finally, the ground colour is wild type and there are small spots of the colour of the very dark allelomorphs. At the same time there is a change in the pattern: at low temperatures there is a small dark patch at the back of the eye; at the higher temperatures there is a speckling of dark spots. The critical test is the study of two different genes affecting the eye simultaneously. When both white and split are present at the same time, the facets showing changes at the white locus are always split, that is, the facets are disarranged, but split facets may be wild type in colour. The genes in order of their distance from the break are diminutive, split and white. When this is kept in mind it appears that the closer a gene is to the point of breakage the more extensive the variegation. Of particular value is the white locus with its series of allelomorphs which dosage experiments have already demonstrated to be hypomorphic to wild type. The process appears to be a sort of inactivation, with the point of breakage acting as a centre from which the disturbance spreads.

The data permit analysis of the question whether the process occurs at one or at many cell divisions. Single white cells occur in the malpighian tubules. This means, as Demerec has pointed out, that the change has occurred in only one of the products of division. Since the variegation is most extensive for the gene closest to the breakage point, as already discussed, it seems most likely that the change occurs at a number of divisions at each of which one of the daughters is unchanged. In extreme cases these unchanged residual cells would be left as small spots in the ground colour of the changed type, and might be interpreted, as indeed they have been, as reverse changes. I have, as yet, found no evidence for this. The data, of which this description is a small sample, are fully accommodated by the assumption that the variegation process starts in the embryonic divisions, and in fact the data of Gowen and Gay on the sensitive period for the temperature effect show that it is just at this time that the change does occur.

We have, then, in the variegation process, an embryological process to deal with. The detailed embryology of the imaginal disks is not yet available; but Poulson's account of the times at which the larval tissues are differentiated with respect to the imaginal disks allows some conclusions to be drawn. The order of differentiation of gonad, malpighian tubule, salivary gland and imaginal disks corresponds very well to the order of increasing extent of variegation. With this series the similarity of the phenomenon to the diminution of chromatin in the embryonic divisions of *Ascaris*, where the germ cells retain the full complement, becomes apparent. The cytological study of the variegation process has reinforced this similarity. It thus appears that the heterochromatic regions play a role in precisely those processes of embryonic division related to the initial differentiation of the nuclei.

Others of the variegated types conform to the same general scheme. The differences between the individual types reinforce the conclusions drawn by varying the conditions within a single one. Variegation for the same gene in different translocations shows that the closer the gene is to the heterochromatic regions the more extensive is the variegation for it, the earlier in development it occurs and the more extreme is the allelomorph, in those cases where allelomorphic series are distinguished.

Mention has already been made of the temperature effect as one of the ways in which variegation may be modified. The process is indeed susceptible to all sorts of modifiers: an unselected stock soon changes the nature of its variegation. But the most potent modifiers are the heterochromaticregions proper. The addition of an extra *Y* to the chromosome complement in many cases almost completely suppresses variegation (Gowen and Gay, Dubinin and Heptner, Schultz, Noujdin). Not only the *Y* but the heterochromatin of the *X* and of the second chromosome, as well as certain of the puff regions, have such an effect. Further analysed, the effect of the heterochromatic regions appears as another case of genic balance. The higher the heterochromatin in proportion to the euchromatic regions the less the variegation. The nature of the interaction is very similar to the temperature effect: the less the heterochromatin the further away from the breakage point the genes affected and the more extreme the variegation. Thus, for example, the perfectly viable *XY* male type described by Demerec and Slysinska, mottled white 258–18, dies at an early stage of development when there is no *Y*-chromosome present (Schultz). Many examples might be given to illustrate further the manner in which genes lying more remote from the breakage point become more and more affected as the amount of heterochromatin decreases. That this is a balance relation follows from such experiments as those with intersexes, in which extensive variegation occurs even with a *Y*-chromosome present.

Thus the behaviour of the heterochromatic regions as modifiers of variegation is quite consistent with their role as inducers of variegation: they affect the progress of the embryonic divisions. An even more striking piece of evidence in this direction comes from the maternal effect of the heterochromatin (*Y*-chromosome, for example), discovered by Noudjin. Here the effect is directly mediated by way of the cytoplasm in which these divisions occur.

But the changes in dosage do not exhaust the modes in which heterochromatic regions affect variegation. The interactions of different translocations with each other constitute another chapter. In this, the limiting case is given by the homozygotes for variegated types. These always show more variegation than do the heterozygotes. Different kinds of effects occur in the combinations of different translocations with each other. For example, the combination of Plum, which shows variegation for the regions of the loci brown and light, with Revolute, which shows a slight light variegation, produces a new type of variegation for a bristle character like straw. Or to take an example of a different type, the combination of white-*vDe*3 (described above) with a more extreme variegated white results in an extensive variegation at 25°. These relations are not as yet very well understood, and it follows that experiments involving the superposition of translocated types upon the original variegation (Dubinin, Stone and Griffin, Panshin) must be interpreted with caution. The results of these workers have shown that the removal of the ever-sporting genes from the heterochromatic regions to regions more conventionally euchromatic results in the suppression of the variegation, as would be expected from the position effect hypothesis. Enhancement of the variegation is produced in other cases, the clearest of which involve new breaks in other heterochromatins. To dissociate position effect and gene interaction in such cases, where the effect of the new translocation by itself is not known, is rather difficult.

From this brief account it is evident that the heterochromatic regions act as general modifiers of the variegation process. Specific modifiers, genes affecting the variegation in special tissues, are also found, although their effects are not so well analysed, and have usually been interpreted to show that the variegation process did not involve changes in the structure of the nucleus but in the manifestation of the genes (Belgovsky). However, such formal analyses of combination effects are difficult at best, and particularly in the case of the variegation process one cannot be sure that the action of a modifier on the bristle effect in variegation is an action on the variega-

tion or on the possible slight bristle allelomorphs produced by it, to give one example. The more direct methods of cytology are necessary here, and it has been possible by the study of the bands in the region of the salivary gland chromosome, in which the variegation is occurring, to trace a cytological correlation with the variegation process.

The example already discussed will serve here also. In the translocation white *v-De*3, the *X*-chromosome bands 3F1 and 3F2 are usually by the side of their normal homologues, so that comparisons are easy at the point of rearrangement. It is clear in this case that the translocated bands are darker in the aceto-carmine stain, and give a more intense Feulgen reaction than do their normal homologues. The position effect is visible, for it extends over a series of bands and its relation to the variegation can be studied. It appears that when variegation is extreme the bands become disarranged; when it is moderate they are darkened; and when it is slight they approach the normal condition.

In collaboration with Dr T. Caspersson this relation has been studied in detail under the ultra-violet microscope, using the methods he has developed for the study of the absorption spectra of cell details. It appears that the relation to distance from point of rearrangement, so striking in the genetic data, is paralleled by the changes in the nucleic acid content of the bands. This has been measured (Caspersson and Schultz); from the measurements it follows that the closer the band to the point of breakage the greater the increase in the amount of nucleic acid over normal. Thus there seems to be an apparent relation between the increase in the nucleic acid content of a band and the inactivation of the genes in the variegation.

Further stages in the process can be seen in the other fragment of this same translocation, where the white region may be followed. At 16° the variegation is maximum, and the cytological study of the white region shows that in most of the salivary gland cells the white locus is directly at the chromocentre, the bands between white and 3F1 are in some cases completely heterochromatic, and in others are not to be found as individual bands at all and are lost as far as can be observed. The sequence of changes seems quite clear and has been followed in a number of translocations. The actual loss is of course difficult to prove, but in these extreme cases seems fairly certain. In less extreme cases (similar to those worked with by Prokofyeva) deficiencies are not observed, although a deficiency of one band correlated with the simultaneous darkening of its neighbour is also difficult to disprove. In any case the data rule out both formal hypotheses concerning mutation, and mechanical hypotheses such as that I proposed some years ago. With the data on the nucleic acid changes it is apparent that the variegation process is a kind of intra-chromosomal diminution, in which the pycnosis of a region leads in the extreme cases to its loss.

From this point of view the maternal effect is particularly interesting. The study of the egg cytoplasm in *Drosophila* has shown (Caspersson and Schultz) that there are large amounts of nucleic acid present there. Moreover, the *XXY* female contains more of these substances than does the *XX* female. The maternal effect of the *Y*-chromosome, causing the decrease in the extent of variegation, is paralleled in the egg cytoplasm by an increase of the nucleic acid content. The ribose nucleic acid of the cytoplasm, connected, as you will hear from Dr Caspersson, with processes of growth and cell division in general, apparently helps the growth of genes in danger of inactivation. The relation of the nucleic acids to the genes then emerges as one of the central problems to be studied in the analysis of the function of heterochromatin.

The effect of the cytoplasmic nucleic acids on the variegation process raises the general question of their relation to the thymonucleic acids of the chromosomes. The hypothesis of Brachet, supported by his studies of the nucleic acids of marine eggs, is that the pentose nucleic acids serve as precursors to the thymonucleic acids. As you will hear from Dr Caspersson, the pentose nucleic acids regarded as characteristic of the cytoplasm are also present in the nucleus: the nucleolus contains them. But the study of the relations in the nucleolus indicates that not only the two types of nucleic acids but their relation to the proteins as well must be considered. Of particular interest from the point of view of the function of heterochromatin are the effects of breakages in the heterochromatic regions, which appear to increase the proportion of ribose nucleotides in the nucleolus of the salivary gland chromosomes. Moreover, the comparison of the ring chromosomes X^{c1} and X^{c2}, the former of which, a variegated type lethal in the *XO* male, has its break within the nucleolar region at 20CD, while the latter with a slight or doubtful variegation has its break outside at 20A, gives promise of another correlation. The accumulation of pentose nucleic acids in the nucleolus is greater in the variegated type X^{c1}, with its break farther within the heterochromatin than it is in X^{c2}. It is as if the process of protein formation in the nucleolus were being slowed down.

With this as a guiding idea a working hypothesis is possible, based on the role of the nucleic acids in the synthetic processes of the cell, which Dr Caspersson will discuss. The heterochromatic regions may be regarded as especially influential in the production of the ribose nucleic acids of the cell; thus their main time of activity is during oogenesis when the reserves are laid down which are to be used in the later em-

bryonic divisions. This activity is cytologically visible as a gradient of the nucleic acids of the cytoplasm around the nuclear membrane where possibly the synthesis takes place. Data are not sufficient as yet to discuss the relation of these cytoplasmic nucleic acids to the mitotic process, and hence to the variegation in detail. But the role of the heterochromatic regions in the variegation process in relation to the nucleic acids necessitates the consideration of the banded structure of the chromosome.

The localization of the genes on the salivary gland chromosomes by different methods has already in a number of cases led to ambiguities. This must mean, as the variegation data surely show, that the band and the interband space are to be regarded as a unit. If it is supposed, and the evidence for such a supposition will be discussed by Dr Caspersson from the chemical point of view, that the complex proteins characterizing a gene are produced by that gene in collaboration with its neighbour at telophase as an interband space, the bases for such ambiguities in localization from chromosome rearrangements are apparent. The abnormal juxtapositions of genes give rise to new types of interband space which cause the position effects of rearrangements. In the heterochromatic regions there is a different type of interband space, consisting, on the basis of evidence to be presented by Dr Caspersson, of a different type of protein. The differences in the synapsis of the two types of region may thus be related to the protein. In the translocations inducing variegation, there is from this point of view the replacement of the specific interband, characteristic of the normal locus, by a non-specific one, whose effect is an inactivation of the gene. The increase of thymonucleic acid in the band is then a symptom of a decreased rate of production of the specific protein, similar to the result in the case of the nucleolus.

It has already been demonstrated that the variegation is an embryological process, and the similarity to diminution pointed out. The question may then be raised whether the normal processes of differentiation of nuclei are in any way related. The nuclei of the different tissues differ not only in their degree of polyploidy, but also in their chromosome structure. It is perhaps worth consideration that some such process of change in gene activity as that induced in the cases of variegation by the heterochromatin may in the normal course of development determine the differentiation of the different nuclei. That inactive nuclei become pycnotic is a byword; the possibility is that the various types differ in the interband spaces, the proteins, formed at and after the telophase. Such an hypothesis would embrace the present data as well as the work on the maintenance of cell type in tissue culture, and the results of the experimental embryologists. The cytoplasm determines the differentiation of the nuclei as Morgan has suggested, and with the variegation process in mind it is possible to make concrete hypotheses as to how this takes place. Thus the study of the function of the so-called inert regions may throw light on how the active ones behave.

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SEARS, E.R., SMITH, L. and O'MARA, J.G. ***Genetic and Cytological Investigations of Polyploid Series in* Triticum *and Related Genera***

Triticum monococcum—living plant exhibit of twenty-one viable seedling mutants; photographs and specimens of twelve mature plant characters; linkage data; photographs of thirteen "sterility mutants", several of which have aberrant meiosis; photographs showing pairing relationships and pollen fertility in plants with reciprocal translocations involving up to ten chromosomes; photographs of a number of chromosome aberrations.

Specimens and photographs showing monosomes, trisomes, and reciprocal translocations in plants obtained from a haploid of *T. vulgare*, and showing nullosomic and tetrasomic derivatives of these plants; specimens and cytological data from hybrids of nullosomics of *T. vulgare* with *T. durum*.

Specimens and cytological data from colchicine-induced amphidiploids.

270

SHEN, T.H. ***Adaptability of Wheat Varieties in Relation to the Various Regions and Breeding Centres in China***

This study confirms the wheat regions established in a previous study and also aids in a determination of important breeding centres of winter wheat in China.

The experiments were conducted during periods of 1–3 years at thirty-five stations from Peiping to Kunming covering the whole winter wheat region.

There were two kinds of tests: (1) the National Regional Test, consisting of the improved varieties already in extension, which was conducted in all thirty-five stations; (2) Regional Tests within regions growing the improved strains and the best local farmers' varieties.

The randomized block arrangement was used exclusively. When the number of varieties was more than twenty-five, they were divided into two groups. The standard error was calculated by the analysis of variance. The comparison of any two varieties in the different groups was made through the common checks of these two groups.

According to the differences in temperature, rainfall, soil conditions, disease reaction and quality, the six regions of winter wheat proposed in the previous study were confirmed. It was found that the six regions can be combined into three main regions, namely, the northern region with semi-arid climate and very severe winter, the central region with semi-arid climate and rather severe winter where spring wheat cannot be grown satisfactorily, and the southern region with humid weather and mild winter where both spring and winter wheat varieties can be grown satisfactorily. The breeding centres suggested on the basis of the results obtained were at Peiping or Taiku for the northern region, Hsuchow for the central and Nanking for the southern region. The more important requirements for the improved varieties in each region were suggested.

271

SHULL, A.F. ***The Nature of the Intermediacy of Adult Intermediate-winged Aphids and its Bearing on the Manner of their Production***

It has long been known that production of wings in aphids can be largely modified, sometimes almost completely controlled, by conditions of light and temperature. Winged aphids have less tendency to produce winged offspring than wingless aphids have. Furthermore, when the gamic phase of the cycle occurs, nearly all the males are produced by wingless mothers, most gamic females by winged mothers.

Occasionally, and under certain conditions frequently, aphids with partially developed wings are produced. This intermediacy of the wings has been attributed to factors acting in late embryonic life, shortly before birth, because the controlling agents have not been effective earlier or later. If, as is assumed in one theory, intermediate-winged aphids start development as of one type (either winged or wingless) and at some point change over to the other type of development, an adult intermediate could be like a typical winged or a typical wingless aphid. That is, the period of transition could be confined to embryonic stages, and the adult might be definitely on the one side or the other. If adult intermediates were found to be like either winged or wingless aphids, the direction of change in the embryo (whether winged to wingless, or wingless to winged) would be known.

By means of the distinctions between winged and wingless aphids indicated in the opening paragraph above, intermediate-winged adults have been tested. The first strain of aphids used in the Michigan studies, tested inconclusively many years ago, indicated that with respect to wing production in their offspring the intermediates might be nearly like the winged or nearly like the wingless type, and that they might produce both males and gamic females in the gamic phase of the cycle. The same strain, after a "mutation" in which its responses were partly reversed and rendered much less definite, now gives the following results. The intermediates produce somewhat more winged offspring than wingless parents do, and many more than the winged parents produce. They likewise produce, very unexpectedly, more males than the wingless parents do.

Another strain of aphids, originally behaving like the first but now probably experiencing a change similar to the "mutation" referred to, produces nearly as many winged offspring as wingless parents do, and many more intermediates than either winged or wingless parents produce. These intermediates have produced no gamic forms, in a period in which wingless parents have produced some males, and winged parents some gamic females.

There is some indication that the response of intermediates depends on the extent to which their wings are developed.

These results are not necessarily opposed to the view that intermediates are produced by a change of development from one type to another, but they require additional assumptions.

A loss of precise control, that is, a spread between thresholds of beginning and of complete determination, would help, and some sort of transfer of this condition from one generation to the next is indicated.

272

SIDKY, A.R. ***Translocation between Sperm and Egg Chromosomes as Evidence that Breakage Precedes Union***

In the course of our work on the relation of translocation frequency to dosage of irradiation and on the relative numbers of double- and multiple-break translocations, one translocation was found between the third chromosome derived from an irradiated spermatozoon and the *Y*-chromosome derived from the non-irradiated egg which that spermatozoon fertilized. That the *Y* had not been present in the spermatozoon was shown by breeding tests of the original translocation-bearing individual, since these showed it to contain but one *Y*-chromosome. Unless we adopt the less probable view that the irradiation had nothing to do with the production of the translocation, or that it gave rise to a long-delayed after-effect whereby translocation by contact was brought about, we must conclude that this case arose as a result of union of pieces of a third chromosome broken by the X-rays in the spermatozoon with pieces of a *Y*-chromosome that happened to have broken spontaneously in the

egg. Thus the case argues strongly in favour of the breakage theory of structural change. The hypothesis adopted is not rendered improbable by the rarity of spontaneous structural changes, since on this view the latter require the coincidence of two spontaneous breaks, which must be far rarer than the occurrence of only one.

273

SIKKA, S.M. *Cytological Investigations of* Brassica *Species and Hybrids*

The study of secondary association of chromosomes in two wild species (*Brassica monensis* and *B. sinapistrum*) has revealed that the probable basic number for the genus is five. The number of satellitic chromosomes and maximum number of nucleoli organized in somatic telophase have been investigated in ten species of *Brassica*. A complete correspondence between the number of satellites and number of nucleoli has been found.

Several species have relatively low chromosome numbers ($2n=16$, 20 and 24). These appear to have originated as allotetraploids, derived from species which have five as the basic number. *B. nigra* has two pairs of satellites and nucleoli, while the four species with 20 chromosomes and one species with 24 have a single pair of satellites. These have presumably lost the extra pair of satellites through mutation.

The presence of six satellites and six nucleoli in *B. juncea* ($2n=36$) indicates that it has arisen as an amphidiploid from a cross between *B. nigra* and one of the 20-chromosomal species. This view has found further support from the study of pairing of chromosomes in the cross *B. juncea* ($2n=36$) × *B. campestris* ($2n=20$), the F_1 of which invariably shows ten bivalents and eight univalents. Similarly, *B. rugosa* ($2n=38$) and *B. napus* ($2n=38$), each having four satellites and four nucleoli, appear to be amphidiploids between species having ten and nine respectively as the haploid numbers and only one pair of satellites.

The meiotic study of some species and interspecific hybrids has revealed the fact that structural changes, segmental interchange and inversion, etc., have also played an important role in species formation in the genus.

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SINGH, B.N. *Certain Aspects of the Physiology of Sex in Higher Plants*

An attempt is made to throw some light on the phenomenon of sex in seed plants by investigation of metabolic drifts in sex organs.

Experimental material was drawn from pure line populations of *Hibiscus esculentus* (hermaphrodite), *Cucurbita pepo* (monoecious) and *Carica Papaya* (dioecious).

March of respiration. There is a fundamental difference between the pistillate and staminate flowers in the case of monoecious and dioecious plants and the stamens and pistils in the hermaphrodite, in the march of respiration from the primordial up to the shedding stage. A high initial level, a more fluctuating rate with advance in age, and a sudden drop after the opening of the flowers characterize the staminate structure.

Chemical analysis. The stamens and staminate flowers have a higher percentage of reducing sugars from the primordial stage onwards, but show a fall after the time of the opening of the buds, while the pistils and the pistillate flowers at this stage show a marked rise.

In contrast to the carbohydrates the total nitrogen is greater in the pistillate than the staminate.

Osmotic concentration. The pistillates start with a higher osmotic concentration and show a decrease in the end, correlated with the slow growth in the beginning and high activity in the end. The staminates start with a lower osmotic concentration correlated with the more rapid early growth, and then increase as senility approaches.

From the results summarized above, it appears that there are definite metabolic differences associated with the initiation and development of the staminate and pistillate parts, whether they are from hermaphrodite, monoecious or dioecious plants. These differences appear to be correlated with the early senescence of the male as contrasted with the more sustained development of the pistillate to the fruiting condition. These results, in conjunction with the photoperiodic and temperature effects on sex expression noted by other workers, point to the conclusions that the potentiality for both types of sex is present at all times, and that the conditions existing within largely influence the expression of one or the other or both types of sex genes.

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SINGLETON, W.R. *Hybrid Vigour and its Utilization in Sweet Corn Breeding*

Hybrid vigour in grain yield of maize was first demonstrated in 1882 by Beal who crossed two open-pollinated varieties and secured an increase in yield of 21 %.

The present method of crossing inbreds was proposed by Shull (1908). In 1909, he outlined the method now in use and foresaw some of its possi-

bilities. East began inbreeding about the same time as Shull and demonstrated remarkable hybrid vigour in crosses of inbreds, and in varietal-inbred crosses (East, 1909). East and Hayes (1911-12) carefully studied hybrid vigour and concluded varietal crossing was the most practical method. East's writings on the subject of hybrid vigour undoubtedly stimulated many workers.

The low yield of inbreds made commercial production of hybrids impracticable. Jones (1918) developed the double cross, and made commercial production feasible. Lindstrom (1931) proposed the top cross (variety × inbred), used widely in sweet corn. About 75–90 % of the sweet corn growing in the United States in 1939 was hybrid. Perhaps 25 % of the field corn crop was hybrid.

The first explanation of Shull and of East was that hybrid vigour was due to a stimulus of heterozygosis. Jones in 1917 proposed "The Dominance of Linked Genes", a factorial interpretation of hybrid vigour, and in 1920 emphasized the importance of selecting superior heredity in the inbred lines. Richey and Sprague (1931) showed that inbreds, secured from backcrossing the F_1 hybrid to both parents, produce as much hybrid vigour as the original lines. These "converged" lines are more similar genetically than the original lines and give support to evidence in favour of dominant growth genes as an explanation of hybrid vigour.

Dobzhansky and Rhoades (1938) suggested the "inversion method" for locating favourable growth genes, by crossing inbred stocks to inversions, which reduce crossing-over; so it is possible to obtain two stocks subsequently, one having ten normal inbred chromosomes and one having nine normal pairs of the inbred chromosomes plus one pair from the inversion stock. Any growth excess of the stock with the inversion chromosomes is evidence for less favourable growth genes of the inbred in the chromosome studied.

We propose another method, which consists of crossing the inbred successively with single chromosome linkage testers, including a small pollen gene to serve as a dominant marker and perhaps reduce crossing-over. The testing will be similar to that described for the inversion method.

There is evidence for a large number of growth genes. Jenkins (1935) showed that two generations of selfing are sufficient to fix the growth factors, and selection is of little value. Jones and Singleton (1935) have corroborated this finding. Apparently the differences between inbreds are due to the number of growth genes originally possessed by the progenitors of the inbred lines.

Hybrid vigour in maize has been established, and open-pollinated varieties are being rapidly replaced by hybrids. As yet there is little experimental evidence on the cause of hybrid vigour.

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Skalińska, Maria. ***The Origin of Polyploidy in* Aquilegia**

In the genus *Aquilegia* the somatic number of chromosomes is 14 in all natural species studied till now. In my experiments carried on during the last ten years two cases of polyploidy in species hybrids were observed: the first tetraploid arose through somatic doubling, while a triploid plant developed from a diploid egg cell of *Aquilegia chrysantha*, fertilized by a normal sperm of *A. flabellata*. Among the selfed progeny of this plant a distinct prevalence of tetraploids appeared, thus the tetraploid number of chromosomes has been here attained in two steps.

In the last case polyploidy was due to the production of an unreduced egg cell by the mother plant, *A. chrysantha*; it belonged to a strain raised from a single plant selfed in 1922 and multiplied by selfing during three generations; the repeated selfing of this allogamous species highly affected both vigour and fertility of the derivative plants. In 1927 meiosis in the mother plant of the strain and of the first derivatives was studied and their pollen was examined; at that time no disturbances in the pollen development were found; the mature pollen was normal without giant (diploid) grains. On the contrary, the pollen of the plants of the third and fourth generations was highly abnormal: it contained a high percentage of abortive grains and besides them giant grains were found in each specimen. Cross experiments of this strain with tetraploids proved that these diploid pollen grains are able to function. Furthermore, a limited number of diploid megaspores were found. The partial sterility of the representatives of this strain of *A. chrysantha* as well as the occasional production of diploid gametes allow us to suspect some irregularities during meiosis; they are caused by the generally abnormal and retarded development of these plants which are characterized by their checked growth, and which manifest a kind of senile degeneration—in a phylogenetical sense. It ought to be emphasized that owing to the frequent production of diploid gametes this strain is able to cross with tetraploids; thus the barrier of incompatibility which exists between the diploid species and their tetraploid derivatives here becomes partially destroyed. Most of the plants obtained in these crosses are tetraploid, while triploids develop only exceptionally. In spite of numerous crosses of tetraploids with wild diploid species, a triploid hybrid, namely, a tri-specific *chrysantha-flabellata-longissima* hybrid, was only once obtained, but this plant is completely male-sterile.

The relatively high production of diploid gametes represents a tendency to frequent polyploid mutations in this senile strain. As is well known, an abnormal

retardation of development, due to internal or external causes in general, seems to represent favourable conditions for a doubling of chromosomes or for other genetical changes. Various factors have been investigated by some geneticists: low temperature, narcotica, as external factors, the immediate effect of which is the checking of growth; and also ageing of seeds—a factor which can be also the cause of mutations in connexion with a retardation of development; another factor seems to be represented by the weakening of an allogamous strain caused by repeated selfing, as in the case of *Aquilegia*.

The appearance of diploid egg cells is here a phenomenon of evolutionary value, as they give rise to polyploid plants; on the contrary the diploid pollen grains are unable to effect fertilization on diploid stigma, and therefore the relatively high production of giant pollen grains has no evolutionary importance in the genus which is cytologically uniform; nevertheless it becomes significant when the first tetraploid individual appears.

277

SLATER, E. ***The Inheritance of Twinning***

Using a collection of psychiatric twins, the incidence of twinning was studied in the families of 281 twin pairs, 103 of whom were of opposite sex. Information about the sibs is complete. Data as to twinship or not are available for 31 % of the 562 parents, 68 % of the 1478 nephews and nieces, and for about 83 % of the 503 children. There is no reason to suppose that the selection used in the compilation of this material affected any particular type of twin, or that its representativeness is vitiated by its incompleteness. As division into uniovular and binovular twins on the basis of anthropological data could not be made in time for the Congress, the author has contented himself with a simple division into same- and opposite-sexed pairs.

The material offers support for Dahlberg's contention that there is an excess of twins among the sibs of twins. The gross incidence of twinning in the total material examined was $2{\cdot}63 \pm 0{\cdot}3$ %, a figure which is certainly above normal. In a small control series of fifty-three families of singly-born psychiatric patients the frequency of twinning was $1{\cdot}158 \pm 0{\cdot}503$ %. The difference between the two series being 2·9 times its standard deviation, it has a considerable degree of significance. This increased tendency towards twinning in the families of twins is, however, only very small, and it seems doubtful whether a difference of this order should be ascribed to genetic factors.

In agreement with previous reports, the author found the frequency of twinning in the families of same-sexed and opposite-sexed twins practically the same. Furthermore, the comparative frequency of opposite twinning shows no deviation from normal in either group of families. In other words, the families of binovular twins show not only an increased tendency towards binovular twinning, but a proportionately increased tendency towards uniovular twinning. The numbers, however, are so small that only a large difference could be detected. The author's conclusion, that if there is a hereditary tendency to twinning it probably manifests itself indifferently in uniovular and binovular twinning, is borne out by another test. When the frequencies of association of opposite-sexed with opposite-sexed, opposite-sexed with same-sexed, and same-sexed with same-sexed pairs within any one family were recorded, they were found to agree closely with expectation on the basis of random distribution and a 35 % relative frequency of opposite-sexed twins.

In respect of the role of the father in twin inheritance the evidence is contradictory. An analysis of the ascendants of the propositi lends itself to the interpretation that the role of the father might be as important as that of the mother. Evidence from the children of twins and the children of their sibs points in opposite direction. Taking the whole lot together, the males show a normal twinning rate of 1·4 %, the females an increased rate of 3·3 %, the difference being 2·2 times its standard deviation. In the author's opinion, existing data do not provide proof for the assumption that the males of twin families are more than normally liable to produce twin children.

Taking all evidence together the author considers that a genetic factor for twinning remains hypothetical. He offers the admittedly highly speculative alternative that twinning may be dependent on environmental factors which may be to some extent what one might call traditional in a family.

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SLIZYŃSKA, HELEN and SLIZYŃSKI, B.M. ***A Salivary Gland Chromosome Map of*** **Drosophila funebris** ***Fabr.***

The identification of the chromosomes in the nuclei of the salivary gland is not difficult; each of the chromosomes shows special characteristics at the free or distal end, and each of them has other morphological peculiarities along the chromosome thread.

The *X*-chromosome, which in the metaphase plate is the longest element, is in the salivary gland of the same length as the average autosome. The *X*-chromosomes often show a close connexion by their heterochromatic part with the nucleolus. The tiny threads coming out of the heterochromatic mass spread

out in the nucleolus. The *X*-chromosome has the highest amount of heterochromatin and therefore the chromocentre belongs mainly to it.

The autosomes do not show as much of the chromocentre as may be seen on the photomicrograph. The longest of the autosomes is the second chromosome, then come the others, all nearly the same length. The sixth is very small and is usually associated with the chromocentre. As a general characteristic of the chromosomes of *Drosophila funebris* in the salivary gland cells it has to be pointed out that they do not form left or right arms. In the metaphase plate they are all rod-shaped except the sixth, which is dot-like. It should also be noticed that they are very easily broken and that the breaking points are always the same. So, for instance, the second chromosome breaks usually in three pieces. In the second chromosome there was found an inversion in a stock established from a fly captured in the southern part of Poland (Tatra Mountains). The details of the chromosome map were shewn in an accompanying chart.

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Smith, G. Ennis. ***Fundamentals of Line Breeding, with Special Reference to Fox Breeding***

The fundamentals of line breeding and inbreeding are explained and illustrated by means of charts and graphs. The application of these methods in the breeding of silver foxes is discussed at length, and advice is offered regarding the actual points which should govern the breeder in his selection of individual animals for such operations.

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Smith, S.G. ***Cytology and Parthenogenesis of* Diprion polytomum *Hartig.***

In November 1930, defoliation of some 2000 square miles of spruce forest by the larvae of a species of sawfly was discovered in the Gaspe Peninsula, Quebec. This has now increased to about 12,000 square miles. Adults obtained were identified as *Diprion polytomum* Hartig, a species previously unreported in America, though known for more than a hundred years in Europe.

The "typical" European and Canadian forms are similar in appearance but differ primarily in their type of parthenogenetic reproduction. In the absence of fertilization, eggs of the former develop into males, whilse those of the latter almost invariably produce females. The rare males (1 in 1200) are almost always sexually functionless. Further, the Canadian form spins its cocoons in the litter below the trees, and the larvae remain dormant for more than a year, whereas the European form as a rule spins in the lower foliage, and more than 95 % of the larvae appear to develop without going into diapause.

The suppression of such a destructive insect is clearly an urgent problem, for not only are the physiological differences which distinguish it from the European form of considerable advantage to it, but it also lacks effective native parasites. In an attempt at control, European parasites are being introduced. By co-operating with the Farnham House Laboratory, the Belleville Laboratory in Ontario has been able to breed and release from 1933 to 1938 242 million insects capable of attacking the sawfly in the egg, larval and pupal stages.

If, as entomologists are led to assume, this insect was originally introduced from Europe, its physiological differences are either secondarily acquired or already exist side by side in different European strains. To settle this question the chromosomes were first studied in both sexes of *D. polytomum* collections from Eastern Canada and Hradec u Opavy, Czechoslovakia. In the Hradec males and females there were 6 and 12 chromosomes respectively; in the Canadian form there were 7 and 14. Thus, despite the difference in the type of parthenogenesis shown by the two, the sex determination in both is of the haplo-diploid type common in the Hymenoptera. In males of the two forms no difference except the chromosome number was found during spermatogenesis. The chromosomes of the first spermatocytes fail to synapse, and the whole complement passes towards the centrosome of the unipolar spindle. At second metaphase each chromosome splits longitudinally and the halves migrate towards the opposite poles of the now bipolar spindle. The second spermatocyte cleaves into two equal-sized spermatids possessing the same number of chromosomes as the soma.

In the female the oogonia are diploid relative to the spermatogonia. In both forms the oocyte chromosomes pair to form the haploid number of bivalents, and their chiasmata entail an orientation of the chromosomes such that the first division must result in a reduction to half the number of chromosomes. It is obvious that, in the Canadian form, the diploid number must be restored by some form of autofertilization.

These preliminary results did not eliminate the possibility of the two forms occurring together in Europe, for if they overlap in distribution, and their progeny mix, this would mask the fact that in one of them parthenogenesis is obligatory and leads to the production of females only. Fifteen collections were therefore obtained from Czechoslovakia, each repre-

senting a different bio-climatic region, and were studied further in England where breeding tests could safely be carried out.

A total of thirty-five females selected from all fifteen regions laid unfertilized eggs which developed into 724 larvae. These all gave small-sized cocoons of which 40 % were spun up in the foliage, and upon reaching maturity all proved to be males. A further group of fifteen females restricted to five of the regions laid unfertilized eggs which developed into 124 cocoons differing from the former group not only in being large-sized but in all being spun in the debris on the floor of the rearing globe. Upon reaching maturity these proved, as expected, to be females, and, in the six instances where tested, produced a second generation which behaved in precisely the same manner. Although numerous attempts have been made to get matings of miscellaneous males with both the obligatory and the facultative parthenogenetic females, no success has been met with.

Twenty-eight of the facultative families have proved to possess the expected male complement of 6 chromosomes, while ten of the obligatory families show the expected female complement of 14 chromosomes.

Clearly then a form exists in Europe which (at least under laboratory conditions) resembles the Canadian form and differs from the European form hitherto recognized in three of the four distinguishing characters, namely, type of parthenogenesis, chromosome number and spinning position. As for the fourth characteristic, diapause, the data thus far obtained are contradictory. A study of 100 individuals comprising the two types of mothers and their progeny, by Mr W. A. Reeks, has shown that structural differences in their genitalia enable their invariable separation. Moreover, since it is the obligatory form which is identical with the Canadian, any doubt regarding introduction from Europe is almost entirely eliminated.

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SPENCER, W.P. ***Ecological Factors and the Distribution of Genes in*** **Drosophila hydei** ***Populations***

Drosophila hydei, a tropical species, has become widely established throughout the U.S.A. in and around cities and towns. In many places it is the dominant form among *Drosophila* breeding on refuse heaps of decaying fruit. Larvae, pupae, and adults are killed by continued freezing weather. In the north the adults overwinter in produce shops, restaurants and fruit cellars. The small winter population then expands through the spring and summer, reaching a peak in the autumn. The species shows unusual tolerance to summer heat. In northern latitudes each town forms a potential focus for an "island" population. Such populations pass through several overlapping generations a year with tremendous fluctuations in population size. The potential effect of migration into the population differs with the season. In response to fluctuations in temperature, moisture, and food supply populations expand and contract year after year. Superimposed on this seasonal ecological pattern are temporary and local disturbances. It is doubtful if these populations ever reach a breeding equilibrium. Thus a mechanism is provided for the rapid diffusion of genetic factors even against selection pressure.

The author has attempted a fragmentary genetic analysis of two widely separated *D. hydei* populations, one living on a large refuse heap of citrus fruit near Azusa, Southern California, and the other in the envirions of Wooster, Ohio. The Azusa population is much the larger, perhaps at peak one hundred times the maximum Wooster population. The hot, dry summer at Azusa and the winter in Wooster constitute the critical reduction periods. The analysis includes the collection and examination of over 50,000 wild flies, and the rearing of over 5000 F_2 pair matings from some 1200 wild flies from the 1937, 1938, and January 1939 Azusa populations, and from the 1937 and 1938 autumn Wooster populations. Inbreeding tests of 100 flies from Gatlinburg, Tennessee, are included. More than 180 cases of autosomal recessives carried in wild flies have been found. In addition, several sex-linked factors and autosomal dominants have been recorded.

The 1938 Wooster population is characterized by the high concentration of a small group of genes; sex-linked vermilion in over 0·25 % of males collected; nicked wings II, four out of 560 genes analysed; rose eye V, three out of 560 genes analysed; grey body III, twelve genes in 1000; and scarlet eye II, three in 1000. Vermilion, grey and scarlet were recovered from the 1937 population several times. The Azusa population shows no such high concentration of specific genes. On the other hand, a significantly larger number of mutant loci is to be found per 100 flies tested from Azusa than from Wooster. The Wooster, Azusa, and Gatlinburg populations have each given a different lot of mutant loci with little overlapping. However, all these populations, and others, agree in carrying a large and indeterminate series of sex-linked bobbed alleles.

We feel certain that the samples taken are inadequate to give an accurate quantitative picture of gene frequencies with the exception of bobbed and vermilion; however, the qualitative results thus far secured make it possible to plan experiments for adequate quantitative tests of yearly fluctuations in specific gene frequencies.

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SPURWAY, HELEN. ***Autosomal Genes Collected from Wild Populations of* Drosophila subobscura**

Autosomal mutations were collected by inbreeding the offspring of females captured after fertilization. The majority of the segregations concerned abnormal wing venations. With few exceptions their behaviour was unpredictable when outcrossed. The distribution of the numbers of segregating F_2 families obtained by inbreeding different F_1's does not agree with the hypothesis that these characters were produced by single recessive mutations carried in the heterozygous condition by one of the grandparent flies. In many families the characters were probably due to several genes, different constellations producing the same phenotype within the same family or even culture. Some segregations of venation, however, can be explained by a single main gene incompletely penetrant and slightly dominant. The remaining segregations were of characters produced by a single recessive gene, though the penetrance of most of these was influenced by the genetic environment, and a few occasionally showed in flies heterozygous for the mutation concerned. The commonest phenotype among them was irregularity of the eye facets. The F_2 segregations of several of the genes responsible for such a character resembled those of wing-vein abnormalities, an unexpectedly large number of cultures segregating but each of these containing only a few abnormal flies.

As was expected from cytological evidence, there are five linkage groups. 40 % or more crossing-over is observed in the four in whicht wo or more loci have been found.

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STADLER, L.J. ***Genetic Studies with Ultra-violet Radiation***

The genetic effects of ultra-violet radiation are of interest chiefly in connexion with three problems.

The first of these is the possibility of breaking down the complex of genetic alterations induced by X-rays. X-ray treatment produces not only apparent gene mutations, but a variety of chromosomal derangements, including deficiencies, duplications, and translocations. It is possible that these effects are necessarily associated, that is, that all are the result of some single basic change produced by the treatment. But it is also possible that they are independent in origin, and that they are always associated under X-ray treatment only because the X-ray is a powerful agent which is able to affect all of the diverse reactions involved. If the former is true, we may predict that somewhere in the spectrum, between the X-ray region which is genetically effective and the visible light region which is genetically ineffective, a point may be found at which genetic effect ceases—and all of these effects will stop at once. If, on the contrary, the associated effects are due to independent phenomena, it is possible that their spectral relations may be different. In this case, points in the spectrum may be found where some of the effects are induced while others are not. This would permit a more or less selective alteration of the genotype, and might make possible the production of mutations without the accompanying chromosomal derangements.

The second problem is closely related. It is the determination of the genetic effectiveness of different ultra-violet wave-lengths, as a possible clue to the chemical nature of the substance which absorbs the radiation producing genetic effects. If, for example, the absorbing substance determining chromosome breakage is nucleic acid, it might be anticipated from the known absorption spectrum of this substance that wave-lengths of about 260 mμ will be most effective in producing breaks, and that effectiveness will decline on the long wave-length side to a negligible value at about 310 mμ. If the genetic alteration results from absorption by some other constituent of the chromosome, the wave-length pattern of effectiveness may be quite different, and the correlation of the genetic data with absorption spectra may suggest substances possibly responsible. If the genetic alterations include diverse phenomena, they may depend upon absorption in demonstrably different substances. Such comparisons cannot be made with X-rays, since X-ray absorption is independent of molecular organization.

The third problem is the genetic analysis of the alterations induced by ultra-violet radiation. It can hardly be assumed that they will include only those types of alteration previously found in X-rayed material, since ultra-violet radiation produces its effects in a manner so different from X-rays. It would be a rash chemist who would attempt to predict the chemical effects of ultra-violet radiation from a knowledge of the chemical effects of X-rays.

I

The "X-ray complex" of genetic alterations includes mutations, deficiencies, and rearrangements. The term "mutation" is here applied to any variation inherited as if due to a change in a gene. The term "deficiency" is applied to any detectable loss of genes. The term "rearrangement" is applied to any detectable change of gene order.

Another type of alteration, which may be independent of these three classes, is the so-called "dominant lethal"—that is, the abortion of the embryo induced by the irradiation of the germ cell. Since the individual

affected is dead before it is detected, there is no possibility of genetic or cytological analysis, and we cannot directly determine the cause of the abortion. It may be due to lethal mutation or deficiency, but it may also be due to any other change in the male germ cell which prevents the development of the embryo.

These four types of alteration are found repeatedly in X-ray experiments, regardless of the organism used or the wave-length applied. So far as I know, no genetic experiment with X-rays, so designed as to permit their detection, has failed to show the presence of all four types of effect.

To determine whether this association is maintained in treatment with ultra-violet radiation, we have made comparative trials with X-ray and ultra-violet treatment of maize pollen, determining the frequency of each of the four effects in the progeny. The ultra-violet first used was the heterogeneous radiation from a quartz-enclosed mercury arc. To find differences in effect within the ultra-violet spectrum, filtered radiations were used, and the differences in spectral response indicated by these experiments were checked by treatments with monochromatic radiations.

The technique used in determining the frequency of the four alterations in maize is as follows: A multiple recessive is pollinated by a multiple dominant, the pollen being irradiated immediately before pollination. The F_1 seeds show the occurrence of embryo abortion and of deficiencies involving any of the marker genes affecting endosperm characters. Deficiencies of marker genes affecting plant characters are shown in the F_1 plants. In addition, deficiencies at unmarked loci are detected by the segregation of defective pollen in the F_1 plants. We have not yet found any deficiency cytologically detectable in the pachytene chromosomes which is not manifested by some recognizable defect in the deficient pollen grains. It is possible, however, that the "deficiencies" so identified may include some mutations causing defective gametophyte development, for such mutations cannot be distinguished from very short deficiencies. Rearrangements also result in segregating defective pollen in the F_1 plants. Pollen segregation due to rearrangement may be distinguished from that due to deficiency either by direct cytological examination of the F_1 plants at meiosis or by certain simple genetic tests. Induced mutations may be detected in the F_2, or, if dominant, also may be detected as aberrant F_1 plants. In practice, the F_2 ears are systematically examined for mutant seed characters, and a planting is made from each ear for the detection of mutant seedling characters.

When pollen is treated with ultra-violet radiation instead of X-rays, the effects are at least superficially similar. The F_1 seeds show numerous endosperm deficiencies and embryo abortions. The F_1 plants show deficiencies of the marker genes, and also include other plants with segregating defective pollen. The F_2 ears yield numerous recessive mutations.

There is one striking difference. In the X-ray series rearrangements are very common; in the ultra-violet series they are rare. For example, in one comparison, in which the doses compared were about equal in frequency of induced endosperm deficiency and embryo abortion, 42 % of the F_1 plants in the X-ray series showed translocation (cytologically detected), and several showed two or more translocations. In addition, 35 % had segregating defective pollen without translocation. In the ultra-violet series, although thirty plants (19·6 %) had segregating defective pollen, there were no translocations. Other comparisons of X-ray and ultra-violet progenies have yielded similar results. Translocations are not always absent in the ultra-violet progenies, but their frequency in proportion to the frequency of plants with segregating defective pollen is always extremely low.

Since the frequency of plants with segregating defective pollen is considerably lower in the ultra-violet than in the X-ray series in these comparisons, it might be suspected that the rarity of translocations is merely incidental to a lower frequency of breakage. If translocations result from breaks followed by re-attachment of the broken ends, they can occur only in cells in which there are two or more breaks. Possibly with ultra-violet treatment the frequency of breakage is too low to give many such cells. If this is the cause of the difference, X-ray doses producing similarly low frequency of segregating plants should be equally low in translocations. Mr Cameron and I have therefore checked the frequency of translocation in X-ray series with doses ranging low enough to bring the total frequency of segregating plants below the ultra-violet level. The ratio of translocations to deficiencies was relatively high throughout the dosage range. This, therefore, cannot be the explanation of the difference.

Is it possible that the few translocations found in the ultra-violet series are spontaneous translocations not resulting from the treatment? Several of the known translocations in maize were found in untreated material, but the spontaneous frequency is unknown. We are now making an accurate determination of the spontaneous frequency in comparison with the frequency in ultra-violet and X-ray series. It seems improbable, however, that the translocations found following ultra-violet treatment are exclusively spontaneous translocations, both because of their number and because of certain peculiarities which suggest a possibly distinctive effect of the ultra-violet.

When the shorter wave-lengths of the ultra-violet spectrum are removed by filtration, another difference

appears. The unfiltered radiation induces both embryo abortions and endosperm deficiencies in rather large numbers. With filtered radiation, from which wave-lengths shorter than λ297 have been removed, there is a sharp drop in the frequency of aborted embryos without a corresponding drop in the frequency of endosperm deficiencies.

This differential reduction in embryo abortion and deficiency suggests the separation of another of the associated alterations. However, we are here comparing the frequency of deficiency in the endosperm with that of abortion in the embryo. It is necessary first to make sure that the spectral relations of deficiency in the embryo and endosperm are similar. These deficiencies are induced in separate nuclei of the treated pollen grain, for in maize the division of the generative nucleus occurs several days before the maturity of the pollen grain. Although the deficiencies induced by ultra-violet are much less frequent in the embryo than in the endosperm, the last filtered radiation which induces endosperm deficiency also induces embryo deficiency, and the first filtered radiation that is without effect upon the one is also without effect upon the other.

The comparison of the same radiations in effect on mutation rate shows the same correspondence; in other words, the yield of mutations varies with wave-length in the same manner as the yield of deficiencies. So far as filtered radiations can determine, the spectral relations of deficiency and mutation are the same. But the longest wave-lengths affecting deficiency and mutation have little if any effect on the occurrence of embryo abortion.

II

The trials with filtered radiations indicated that genetic effectiveness, for the production of deficiencies and mutations, extends through the ultra-violet spectrum only to about 310 mμ, and that within this range the shorter wave-lengths were considerably more effective than the longer. An accurate determination of the effects of individual wave-lengths, suitable for the comparison of genetic effect with the absorption spectra of specific substances, of course requires the use of monochromatic radiation. By the use of a special monochromator of high light-gathering power and of a capillary mercury arc of high intrinsic brilliance, it is possible to apply monochromatic radiation in sufficiently high intensity over the rather large area required to hold in a single layer a sample of pollen sufficient for the pollination of an ear.

The effect of monochromatic radiations upon the frequency of deficiency may be determined with considerable precision, since there are many known genes in maize with clear-cut effects upon endosperm characters, and deficiencies for these genes may be identified in large numbers. Dr Uber and I have recently made a rather extensive study of these effects. Since the results have not yet been published, I will summarize them briefly.

A serious difficulty in all such studies is the unavoidable loss by absorption which occurs before the radiation reaches the point at which it produces its effect. Even in irradiating uncovered pollen grains lying in a single layer, there is a very considerable loss in intensity in the passage of the radiation through the pollen-grain wall and through the material overlying the gametic nucleus. This loss varies rather widely at different wave-lengths, so that equal doses in terms of the energy incident at the surface of the pollen grain are by no means equal in energy incident upon the chromosomes.

In the mature maize-pollen grain there are two sperm nuclei, one of which will fuse with the egg to produce the embryo while the other will fuse with the polar nuclei to produce the endosperm. The nuclei are eccentrically located, and, in a sample of pollen grains orientated at random, the distance from the upper surface to the position of the nuclei will vary greatly in different pollen grains. This factor is of little importance with highly penetrating radiations such as X-rays or γ-rays. But ultra-violet radiation is so highly absorbed that there is a great difference in the dose which reaches the uppermost and the lowermost possible position of the nuclei. In other words, in a sample of pollen grains given a uniform dose, some nuclei will be very heavily treated and others very lightly treated, depending upon the orientation of the grain.

This has several important effects. The most significant for our present purpose is a flattening of the dosage curve for specific deficiencies. For example, consider a layer of pollen grains oriented at random, and consider a dose applied in ten successive exposures of one unit each. The first unit may produce the deficiency in any of the pollen grains, and its hits will tend to occur in the most favourably oriented ones. Later units may produce additional deficiencies only in the unaffected pollen grains remaining, which offer on the average a lower probability of hits because of their less favourable orientation. Before the last unit is applied, most of the favourably oriented pollen grains may have been hit, and further treatment may produce no appreciable effect.

The extent to which this factor will apply depends upon the rate at which the radiation is absorbed in the pollen-grain contents. This varies widely for the wave-lengths compared. Absorption is relatively high for λ265 and low for λ297.

Both wave-lengths show a flattened dosage curve, but the flattening begins much earlier for λ265. In comparing these two wave-lengths in genetic effect, the

result of the comparison depends entirely upon the dose chosen. Equal doses of 2000 ergs/mm.² show λ265 much more effective; equal doses of 16,000 ergs/mm.² the reverse.

This indicates that comparisons should be made at the lowest dose practicable, since this error is at its minimum in the lowest doses. Even in the most favourably oriented grains, the radiation must penetrate some overlying material, and therefore the results, even at the lowest doses, are distorted to some extent by this factor.

Comparison of monochromatic radiations at the rather low dose of 2000 ergs/mm.² gives the results shown in Fig. 1. The most effective wave-length is

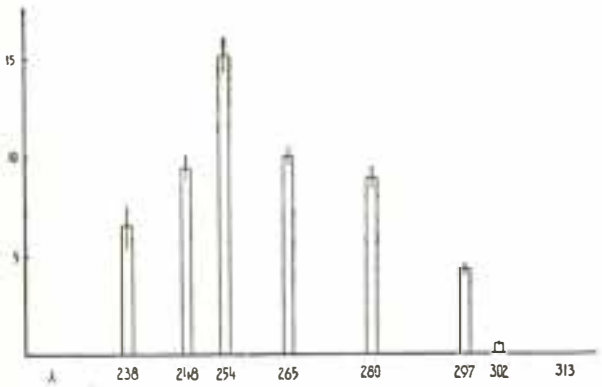

Fig. 1. Relative frequency of endosperm deficiency under monochromatic ultra-violet radiation. (Dose 2000 ergs/mm.²)

λ254, the effect diminishing with both shorter and longer wave-lengths and reaching a negligible value at λ302.

Although λ297 and λ302 are low in effect at this low dose, they may be shown to be distinctly effective when higher doses are used. Dosage as high as 64,000 ergs/mm.² is tolerated at λ297, and at this dose the endosperm rate is very high, more than three times as high as the highest rate shown on the graph. At this dose λ302 yields about one-third as many deficiencies as λ297. Its greater tolerance permits the application of a dose four times as high, and with this dose λ302 yields almost as many deficiencies as λ297 at its maximum.

The next wave-length, λ313, has little or no effect. Doses of more than 1,000,000 ergs/mm.² have been applied at this wave-length with no appreciable injury to the pollen and with only a very slight increase in the frequency of endosperm deficiency. Since the radiation from a single monochromator is not absolutely monochromatic, this small effect might be due to slight impurities of shorter wave-lengths. By using filtration to remove most of the shorter wave-length energy before the radiation was passed through the monochromator, it was possible to remove all but a trace of the genetic effect. This wave-length therefore has at most a very slight genetic effect, and it may be wholly ineffective.

Thus the spectrum of genetic effectiveness, so far as it may be determined within the limitations which have been mentioned, is not greatly different from the absorption spectrum of nucleic acid. Unfortunately, the material is not suited to a rigorous physical analysis, and it is to be hoped that similar determinations of genetic effect may be made with material in which the dosage at the chromosomes may be more accurately determined.

III

In considering the genetic effects of X-rays and ultra-violet radiation, we have noted the pronounced differences in the effect upon translocation and embryo abortion. Deficiencies and mutations are produced by both kinds of radiation. But are the deficiencies and mutations produced by ultra-violet radiation wholly analogous to those produced by X-rays? In the case of the deficiencies at least, it is obvious that they are not.

Some of the differences may be seen in the F_1 ears produced by the two kinds of radiation. Both show numerous deficiencies affecting endosperm characters. But among the deficiencies produced by ultra-violet there is a high proportion of fractionals, including many in which the deficient sector makes up about half of the endosperm, others with deficient sectors somewhat smaller or larger. This is the distribution of tissue to be expected if the two-celled pro-endosperm consists of one deficient and one non-deficient cell, for endosperm development is not so regular as always to maintain the half-and-half distribution to maturity. If the treated chromosome is directly affected we must assume that it is predivided in the mature gamete and that the induced deficiency usually affects only the half-chromosome.

In the X-ray progenies, however, most of the deficiencies affect the endosperm as a whole. In addition, there is a substantial minority of fractionals, but most of these are seeds in which the deficient sector includes almost the entire endosperm, the non-deficient region being represented by one or more islands of tissue usually amounting in total to very much less than half of the endosperm. The distribution of tissue is that which would be expected if a chromosome fragment may occasionally escape elimination through one or more cell divisions and then be restored to normal mitotic distribution. If the endosperms with a very small non-deficient portion represent recoveries after several cell divisions, those with larger non-deficient sectors may represent the same phenomenon after only one or two divisions. It is possible, therefore, that many or all of the frac-

tionals in the X-ray progenies may result from deficiencies affecting the chromosome as a whole.

Whether or not the mode of origin of the fractionals is as suggested, the differences between the two radiations in the frequency of fractionals and in the type of fractionals is unmistakable. A typical comparison is shown in Fig. 2.

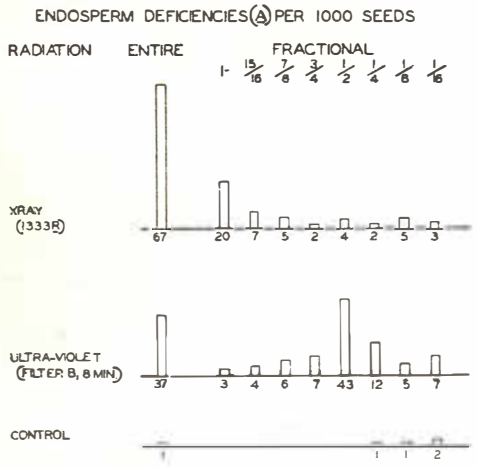

Fig. 2. Relative frequency of entire and fractional endosperm deficiencies of *A* induced by irradiation of pollen.

With X-rays the total frequency of all fractionals is less than that of entire endosperm deficiencies, and the largest class of fractionals is that in which almost the entire endosperm is deficient. With ultra-violet, fractionals are three times as frequent as non-fractionals, and they show almost a normal distribution about the half-endosperm class. These characteristic differences in relative frequency and type of fractionals apply regardless of the dose of X-ray or ultra-violet radiation applied.

Thus, according to the interpretation sometimes applied in analogous cases, the X-ray data show that the chromosome is undivided at the time of treatment, at least in most pollen grains, while the ultra-violet data show that it is divided at the time of treatment, at least in three-fourths of the grains. But the time of treatment in the two cases is precisely the same.

It might be supposed that the two radiations bring about their effects in different constituents of the chromosome. Perhaps the ultra-violet radiation affects the chromonemata, which have predivided, while the X-rays affect some other portion of the chromosome, which is still undivided at the time of treatment. If the deficiencies induced by ultra-violet represent both whole-chromosome and half-chromosome breaks, we might hope for some possible spectral difference in the two phenomena. In other words, we might expect a different ratio of entire to fractional deficiencies at different ultra-violet wave-lengths. The data for monochromatic radiations, however, give no indication of any such difference.

Another striking difference between the deficiencies induced by the two agents is the extremely low frequency under ultra-violet radiation of deficiencies affecting the embryo. With heavy doses the frequency of endosperm deficiencies marked by *A*, *Pr* and *Su*, the marker genes commonly used, sometimes exceeds 40 %. These markers identify deficiencies only on three of the 20 chromosome arms irradiated, and must fail to be included in many of the deficiencies even on these three arms. The frequency of deficiencies which would be identified if all loci could be marked must therefore be several hundred per cent; that is, the average endosperm must have several deficiencies. But in the embryos of the same seeds deficiencies are much less frequent. The occurrence of unmarked deficiencies in the embryo can be determined only by growing the plants to the flowering stage and examining for the resulting defective pollen segregation. When this is done the frequency of plants with segregating pollen proves to be only 20 to 25 % from the highest doses. Even if we assume that every seed which failed to yield a pollen specimen was a deficiency (including those with aborted embryos, those which failed to germinate, and those which gave plants from which no pollen specimen could be obtained), the maximum frequency of possible deficiencies is only about 30 %. Among these assumed deficiencies, many involve only slight defects in pollen development, and some of these have been examined cytologically and found to show no deficiency visible at pachytene. It is possible that these may be mutations affecting gametophyte development, and if so, this would reduce still further the frequency of deficiency in the embryo. On the other hand, many cytologically visible deficiencies have been found, and it is certain that there is a real increase in the frequency of cytologically demonstrable deficiencies in the F_1 plants. Unquestionably, deficiencies are induced in the embryo, but the rate is far below that found in the endosperm.

This discrepancy is shown also by the genetically marked deficiencies. Endosperm deficiencies of the gene *A* are very common, and with the heaviest doses they sometimes occur in 20 % of the seeds. The gene *A* also affects the colour of the seedling. If deficiencies were produced with the same frequency in the embryo as in the endosperm, we should expect the F_1 seedlings to include many showing the absence of the *A* gene. Such seedlings occur, but they are extremely rare. In ultra-violet progenies grown from seeds, which included 493 endosperm deficiencies of *A*, only five deficiencies of *A* were found in the F_1 plants.

This discrepancy does not appear in X-ray material.

Seed from moderately X-rayed pollen yields an extremely high frequency of deficiencies, and many of the plants have two or more deficiencies. In addition, a considerable percentage of the seeds so treated are germless, and many others yield seedlings too defective to reach the pollen-shedding stage. The frequency of *A* deficiencies in the seedlings is almost equal to the frequency of *A* deficiencies in the endosperm, and the slight reduction is probably no more than may be accounted for by the higher deficiency rate in the embryos which fail to yield F_1 plants.

The explanation of the low rate of embryo deficiency with ultra-violet is still an open question. About three-fourths of the endosperm deficiencies are fractionals, and we may imagine that when a fractional occurs in the embryo, the non-deficient fraction may outgrow the deficient fraction. But the discrepancy is too large for this to be the whole explanation; among the seeds which yielded only five *A* deficiencies in the F_1 plants there were more than a hundred non-fractional *A* deficiencies in the endosperm. Another possibility is an actual difference in the frequency of the primary effect of treatment on the two sperms of the treated pollen grain, although these show no visible difference in structure or position. A third possibility is a difference in some secondary effect which occurs after fertilization, for the course and rate of early development are very different in endosperm and embryo. Whatever the explanation, the phenomenon is another indication of a fundamental difference in the deficiencies induced by X-rays and by ultra-violet.

These differences and others which cannot be described here suggest that the deficiencies induced by ultra-violet are of a different sort from those with which we are familiar in X-ray experiments. Direct cytological examinations of ultra-violet induced deficiencies, so far as they have gone, confirm this expectation. These deficiencies have been studied at pachytene by Dr W. R. Singleton and Miss F. J. Clark of the Connecticut Agricultural Experiment Station, Dr L. H. Hill of the U.S. Department of Agriculture, and Dr K. M. De Boer of the University of Missouri. I am indebted to these investigators for permission to refer to their results before publication.

All of the deficiencies cytologically detectable at pachytene have the appearance of terminal deficiencies. The distinction between terminal and non-terminal deficiencies is not positive in maize, because of non-homologous pairing, and we are consequently inclined to distrust any single case. Among X-ray deficiencies apparently terminal cases are not rare, but an alternative possibility for each case is non-terminal deficiency with one break so near the end that pairing never occurs in the distal segment.

The number of apparently terminal deficiencies with ultra-violet is now too large to permit this interpretation unless we assume a special tendency for ultra-violet radiation to produce deficiencies in which one break is always very near the end of the chromosome. Singleton has previously reported six cases, and the total number of additional cases found to date by the investigators mentioned is fourteen. Not a single case has been found of apparent non-terminal deficiency. A random sample of twenty X-ray deficiencies would have included many such cases.

What is the genetic nature of the induced embryo abortion? In the first place we must recognize that it is probably not a single phenomenon. There is no more reason to look for a single genetic cause of embryo mortality than for a single genetic cause of plant mortality. There may be single genes which are indispensable; there probably are single chromosome segments, the loss of which is lethal; and it is almost certain from the extremely deleterious effects of certain viable deficiencies, that there are coincidences of deficiencies which must be lethal. Since the frequency of embryo abortion induced by X-rays increases very rapidly at high doses, it has seemed most probable that coincidences of deficiencies were the major factor.

The specific response to the shorter wave-lengths suggests that this may not be the chief source of abortions, at least for those induced by ultra-violet treatment. Among the aborted embryos occurring at high doses there may be some from deficiencies; but if these were all, there should be a consistent relation between the frequency of deficiency and that of embryo abortion. The excess of aborted embryos at short wave-lengths may represent abortions resulting from some other effect on the treated sperm. It is not necessarily true that the genes and chromosomes are all that the sperm contributes that is essential for embryo development. Some other constituent, if essential to normal fertilization or to normal development, might, when destroyed or modified, lead to failure of embryo development.

There is, however, another possible way of accounting for a special incidence of embryo abortion at the shorter wave-lengths as a result of deficiency, if we assume that coincidences are often involved. The unequal exposure of the gametes in different pollen grains, which was discussed in relation to the flattened dosage curve, would lead also to increased coincidence of independent effects. This would be at its maximum in treatments with the wave-lengths which are most highly absorbed in the pollen-grain contents—that is, with those which show the greatest flattening of the dosage curve. These are, in fact, the wave-lengths at which embryo abortion is found most frequently. Several F_1 populations have been grown from cultures relatively high in embryo

abortion, in order to determine the frequency of deficiency in the embryos which were not aborted. The percentage of deficient plants found is usually lower than the percentage of aborted embryos, and only a very small proportion involve coincident deficiencies. The number of aborted embryos seems far too large to be accounted for in this way.

A possible explanation is that many of the aborted embryos are haploids which fail to survive the embryonic stage. A few haploids have been found in progenies from ultra-violet treated pollen. It seems probable that haploids would usually be inviable in maize, because of the presence of recessive lethals which may be carried in the heterozygous state, and probably because of additional haplo-lethals which may be tolerated by the diploid even in the homozygous state. A treatment inducing haploids therefore might show its effect chiefly by the production of an excess of aborted embryos rather than by the production of detectable haploids. If so, the specific spectral relations of embryo abortion may indicate the substance in the male germ cell which is responsible for this effect.

Since the haploids which survive occasionally produce diploid sectors, it should be possible to derive from them homozygous lines free from haplo-lethals, in which this hypothesis may be tested.

IV

The ultra-violet results thus indicate that the dependence of mutation upon chromosome rearrangement has been over-emphasized. They, of course, give no cause to question the identification of specific mutations as the result of rearrangement, but they show that mutations also may be produced in high frequency by a treatment which has little if any effect on the occurrence of rearrangement.

It is plausible to assume that mutations are of various types; that position effects, deficiencies, and duplications incidental to generearrangement make up a considerable proportion of the mutations found in X-ray progenies; and that the mutations induced by ultra-violet treatment are largely or wholly of other types. This suggests the importance of a critical comparison of the ultra-violet mutations with X-ray mutations and spontaneous mutations.

All current theories of the mechanism of chromosome derangement imply a close relationship in origin for translocations and deficiencies. This can hardly be valid for deficiencies in general, though it may be so for certain types of deficiency, if the deficiencies induced by ultra-violet are largely of other types. The observations summarized above show that the ultra-violet deficiencies as a group differ from the X-ray deficiencies as a group, but critical cytological study of the deficiencies in much larger numbers is necessary to determine the occurrence and proportions of the various types among the deficiencies induced by the two agents.

In view of the relative rarity of translocations in the ultra-violet progenies, it might be argued that gene rearrangement is dependent upon some reaction which may be energized by X-rays but not by ultra-violet radiation. I do not believe that this argument is justified by the present evidence. It involves the assumption that the mutations and deficiencies induced by ultra-violet are analogous to those induced by X-rays, for the only indication that the dose of ultra-violet applied is comparable with that of X-rays is the fact that it produced comparable numbers of mutations and deficiencies. It must be remembered that the doses of the two radiations compared are not based upon any physical determination of equivalence, but are simply determined by the amount of each treatment which the pollen will tolerate. Assuming that the rearrangement reaction is induced as readily by ultra-violet as by X-rays, it would, of course, be possible to obtain high rates with X-rays and low rates with ultra-violet by the use of a disproportionately low dose of ultra-violet in the comparison.

One may ask, "What is the relative yield of translocations from X-ray and ultra-violet doses equal in the amount of energy absorbed?" But this question has no meaning except in terms of some assumed absorbing unit. We may calculate doses equal in absorption by the entire pollen grain or by the entire gametic nucleus, or by the molecule of nucleo-protein or of nucleic acid, or by the specific bonds within the molecule in which the ultra-violet energy is presumably absorbed. In the present state of our knowledge of the chemical composition of the gene and chromosome, and of the photochemistry of very complex molecules, such calculations have little meaning.

We are, therefore, forced to use some biological criterion. We may, for example, compare the rearrangement rate from doses equal in frequency of induced mutation or deficiency, and it is this comparison which shows a marked excess of rearrangements from the X-ray.

This shows that the rearrangements differ in spectral relations from the mutations and deficiencies. The difference may be due either to a sharply reduced response of rearrangement to ultra-violet or to the occurrence in the ultra-violet series of classes of mutations and deficiencies which are absent or rare in the X-ray series.

In the case of the mutations, there is no evidence of any genetic distinction between those produced by ultra-violet and those produced by X-rays. But there are few criteria for the classification of types of mutation, and this similarity therefore may be illusory. In

the case of the deficiencies it is possible to demonstrate a qualitative difference *en masse* between those from X-rays and those from ultra-violet. Deficiencies of the type related to translocation may be no more frequent in the ultra-violet progenies than are the translocations themselves. If so, the low rate of translocation following ultra-violet treatment may be due not to any spectral limitations but merely to the relatively low dose to which we are held by limited tolerance.

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STARK, MARY B. ***The Origin of Certain Hereditary Tumours in* Drosophila**

In all animals that pass through distinct stages of metamorphosis, where certain organs or systems of organs are replaced by a complete set of new organs or systems in the final adult stage, there will be found groups of embryonic cells or rests lying latent during the functional life of the original embryonic organs and systems, which in due season will develop into the adult structures.

From a study of serial sections of many larvae of *Drosophila* with hereditary tumours, it has been definitely ascertained that some of the tumours arise from these embryonic rests latent in the wall of the digestive tract. These tumours are epithelial in character and cause the death of one-half of the males. These same embryonic cells in another strain of *Drosophila* and at a later stage, when they are capable of a degree of differentiation, become encapsulated by a new growth of connective tissue, thus giving rise to a benign tumour which is not sex-linked.

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STEIN, EMMY. ***Über erbliche, durch Radiumbestrahlung erzeugte Gewebe-Entartung in* Antirrhinum siculum *und in Petunien***

Unter den aus bestrahlten Samen hervorgegangenen (R) Pflanzen sind Periklinal-Chimären aufgetreten, deren Zellstruktur nur in bestimmten Embryonalschichten verändert ist. Zellen, Kerne und Kernkörper sind auffallend vergrössert, ohne Vermehrung der Chromosomenzahl. In einzelnen Fällen kommt es zu Exzessen, bei denen Zellen, Kerne und Kernkörper ins Riesenhafte anschwellen um dann zugrunde zu gehen. Die Chimären von *Antirrhinum siculum* haben dieselbe morphologische Eigenart, die früher bei den in gleicher Weise erzeugten *A. majus* Chimären beobachtet wurde. Pflanzen mit veränderter Zellstruktur der Epidermis sind schmalblättrig, während die Veränderung der zweiten Embryonalschicht sich in Farb- und Formdefekten äussert.

Viele R Pflanzen waren pollensteril. Bei *A. siculum* trat in einer F_2 Nachkommenschaft, aus Kreuzungen mit der unbehandelten Sippe, eine Rezessiv Mutante auf, deren Gewebe immer regellos wachsen. Sie entwickelt nur winzige, verkümmerte Blattorgane, wird *ca.* 1 cm. hoch und geht früh zugrunde.

Unter entsprechenden F_2 Petunien sind 1938 Einzelpflanzen gefunden, deren Zellen hier und dar zu Wachstumsexzessen neigen. Die Entartungen sind deutlich, aber weniger extrem und umfangreich, als die früher bei *A. majus* beschriebenen. Andere F_2 Petunien haben in allen Embryonalschichten auffallend vergrösserte Zellkerne und Kernkörper. Für den Erbgang der bei Petunien genannten Veränderungen wird in diesem Sommer noch einige Klärunge erhofft.

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STEINBERG, A.G. ***The Growth Curves of Bar and Wild-type Eye-disks of* Drosophila melanogaster**

Ever since its discovery by Tice in 1913 the Bar mutation of *Drosophila melanogaster* has been the object of a large series of investigations. Despite this vast amount of work we have little or no direct knowledge of the development of the Bar eye. The present paper is a preliminary report of experiments under way in an attempt to supply these much-needed data.

The stocks used in the experiment were an inbred Bar stock and an inbred Florida wild-type stock with which the Bar stock is isogenic. Eggs were collected over a 24 hr. period at 25° C. All subsequent development took place at 27 ± 1° C. All ages were calculated from the time of hatching and are accurate to within ± 1 hr. Camera-lucida drawings were made of the living eye disks immediately after they were dissected from the larvae. The areas of these drawings were then measured by means of a planimeter. Measurements were made at 12 hr. intervals from 36 hr. after hatching until 84 hr. after hatching, at which time approximately one-half the larvae had begun puparium formation. Only those larvae which had not formed prepupae were used, consequently the 84 hr. measurements may be somewhat smaller than they would be in a random sample of 84 hr. old larvae.

The data establish the following: (1) that the cephalic complex of Bar is already smaller than that of wild type at 36 hr. after hatching (Bar = 154·1 ± 4·0 and wild type = 177·8 ± 4·8); (2) confirming Medvedev's finding, the cephalic complex separates into the optic and antennal disks between 36 and 48 hr. after hatching; (3) that the optic disk of Bar is smaller than

that of wild type at the time of its separation from the antennal disk (Bar = 345·3 ± 6·7 and wild type = 543·6 ± 9·1); (4) that the initial growth rate of both Bar and wild type is high and that the rate decreases with increasing age; (5) that the growth curves of Bar and wild-type eye disks are the same throughout the period under observation.

It appears therefore that the influence of Bar on facet number probably occurs long before the "temperature effective period" (the T.E.P. is approximately 40–60 hr. after hatching at 27° C.). Consequently it seems highly likely that the effect of Bar during the T.E.P. is not directly on the facet-forming process, but is of a more general nature, such as to cause the optic disk to be more sensitive to temperature changes than is the wild type during this period.

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STEWART, J.L. ***Livestock Improvement in the Northern Territories of the Gold Coast***

The native cattle of this area were unhumped, small, hardy, and very resistant to enzootic disease but, from the economic point of view, were undeveloped. General conditions of husbandry were inferior, except in some districts where Fulani herdsmen were employed. Improvement schemes have been directed to improve size and conformation, while retaining hardiness and disease resistance. Earlier experiments with Herefords and Shorthorns having been unsuccessful, work is now carried out with other West African types of cattle and by selection within the local types; the best results have come from using short, deep-bodied zebu bulls. Their hybrids with the native cattle are known as Sangas and are intermediate in character and breed fairly true. Another unhumped variety, of superior conformation and disease resistance, is the N'Dama, prominent in the Fouta Djallon mountains of French Guinea. A type of N'Dama Sanga is being developed to suit conditions in the north.

An important part of the improvement schemes has been the distribution of communally owned, improved bulls to the village herds. A number of Native Administration farms have been established and stocked with the best local cows procurable and bulls supplied by the Department of Animal Health from its farm at Pong Tamale; improved methods of husbandry are also demonstrated. (At one farm a specific local variety is stocked; this is the White Builsa, a short, stocky animal of good conformation and white colour with black points.) In approved village herds, using communal bulls for some years, the weight of bullocks has increased from about 5 cwt. to 6½–7 cwt., with improved conformation.

Pig improvement was by means of Middle White grades from the native pig, but this cross was found too fat, and during the last ten years Large Whites have been used, pure-bred and cross-bred pigs being bred at Pong Tamale for distribution to native owners direct. These white pigs, kept under natural conditions and grazing during the day, do not suffer from "sun scab". It is proposed to establish a herd of Large Black pigs on a farm in the coastal plains; this has been a very successful breed in French West Africa.

Rhode Island Reds and Black and Brown Leghorns are being used in the poultry improvement schemes. At Pong Tamale pure-breds are reared and also crosses between good type native hens and Rhode Island Red and Black Leghorn cocks. The pure European types only do well under progressive management, but the cross-breds do well and approach the pure-breds in size and egg production. Distribution of cross-breds occurs from the Native Administration farms.

288

STOMPS, T.J. ***On Artificially Produced*** **Oenothera Lamarckiana gigas**

By means of colchicine treatment the writer has succeeded in doubling the number of chromosomes in *Oenothera Lamarckiana*. He obtained two plants which were absolutely identical with the true *gigas* race Hugo de Vries derived from his *Oe. Lamarckiana*. There can be no doubt therefore that *Oe. Lamarckiana gigas* is simply a doubled *Oe. Lamarckiana* contrary to the writer's earlier opinion and that of de Vries who considered his *gigas* type to be a progressive mutation.

289

STOUT, A.B. ***Hybridization and Selective Breeding in the Genus*** **Hemerocallis**

The recognized species of *Hemerocallis*, about fifteen in number, possess wide diversities in such important features as stature, habits of growth, season of bloom, and flower characters (as size, colouring and flowering behaviour). Except for the several triploid clones in the species of *H. fulva*, all species are, it appears, diploid with $2n = 22$ chromosomes. There are some interspecific hybridizations that fail and certain F_1 progenies have not yielded seeds to any pollination; but many hybridizations between species that are widely different have been accomplished. As a rule, in the F_1 hybrids there is either some degree of dominance or some degree of intermediate expression

for the sharply contrasted characters of species used as parents. In only a few cases do decidedly new and unexpected characteristics appear in the F_1.

But numerous rather distinctly new expressions for various characters are obtained when hybridizations, especially those which involve several species in the parentage, are followed by selective breeding. These may be due (1) to recombinations which involve two or more pairs of contrasted characters, or (2) to distinctly new expressions. One example of the latter is the intensification of pigmentation which resulted in flowers which have dark mahogany red colouring. First there was hybridization which involved yellow-flowered species and species with fulvous flowers. The F_1 had pale fulvous flowers and of the F_2 none had flowers that were darker than the more fulvous parent. Then plants which showed the greatest degrees of anthocyanin pigmentation were used as parents in further breeding and in backcrossing. In the fifth generation a progeny of sixteen plants were obtained, all of which had degrees of dark red pigmentation not seen hitherto in any day-lily. The various complementary factors which interact to intensify anthocyanin pigmentation in the flowers were brought together by hybridization and by the subsequent selective breeding into relations which produced a new type that had hitherto not been in existence. Thus in selective breeding after hybridization of *Hemerocallis* various specific characters may be modified for the development of distinctly new horticultural types of day-lilies.

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STRANDSKOV, H.H. ***Inheritance of Internal Organ and Skeletal Variations in Guinea-pigs***

From a genetically heterogeneous stock of guinea-pigs, two lines of brother-sister matings, family 2 and family 13, were started in 1906 and carried as brother-sister matings for twenty-four and thirty-one generations, respectively. At the end of these generations each line should theoretically have been over 99 % homozygous. The internal organs and skeletal parts of twenty males and twenty females of each line were weighed and measured and the quantitative data were compared statistically.

Family 13 is significantly heavier and longer than family 2, and in each family the males are heavier and longer than the females.

The liver, lungs, and heart in family 13 are heavier than those in family 2. These organs are also heavier in the males than in the females. The thyroids in family 2 are longer, although lighter. This seemingly contradictory statement is explained by the fact that the thyroid in family 13 is thick and compact, whereas that in family 2 is loose and strung out. The adrenals in family 13 are flat and thin and show a characteristic indentation. In family 2 they are triangular and thick in cross-section. The spleen in family 2 is much longer and relatively narrower. There is also a sex difference with respect to spleen size, that of the female being much longer.

Most of the skeletal measurements in family 13 are greater than those of family 2, except the depth of the skull in the palatine-frontal region, and the length of the humerus, femur and tibia, which are significantly greater in family 2. The bones of the males are longer than those of the females except the scapula and the humerus, which are of the same length in the two sexes.

The occurrence of clean-cut differences between the two families and the persistence of these differences through many generations make it fairly certain that the differences observed have a genetic basis. The positive correlations between body weight and the weights of the liver, the lungs, and the heart, suggest that the weight of each of these organs is determined to a large extent by general body-size factors. On the other hand, the differences found in the thyroids, adrenals, and spleen suggest that the size and shape of each of these organs may be affected by genetic factors quite independent of those which determine general body size. This may also be said for the length of the humerus, femur, and tibia and, therefore, probably for the length of any other bones of the body.

The sex differences in body weight, body length, bone measurements, and spleen size are probably due to secondary effects of sex-determining genes.

291

STRONG, L.C. ***Cancer of the Mammary Gland in Mice; is it Genetic, Congenital or Acquired?***

The age distribution and the parentage of individuals showing spontaneous carcinomas of mammary tissue is significantly influenced by the diet upon which the mice have been kept.

Cancer of the mammary gland in mice is determined by an original contribution from the germplasm which has been continuously influenced by forces from the diet (before birth and up to the time that malignancy shows itself).

Cancer is consequently not a "unit character", and a classification of cancer and non-cancer individuals in a hybridization experiment is probably not justified. Further work on the nature of the susceptibility-to-cancer and the resistance-to-cancer states is

indicated before a final analysis on the part played by genetic determiners in these states may be made possible.

292

SUTTON, EILEEN. ***The Structure of Euchromatic and Heterochromatic Translocations in the Salivary Gland Chromosomes of*** **Drosophila melanogaster**

Studies have been made with the object of determining the structure of euchromatic and heterochromatic bands when their position in the salivary chromosomes is changed. The material studied includes $Dp(1)^{264-58}$, a duplication in which a small euchromatic segment of *X*, 3B3–4 to 3D5–6 inclusive, is inserted in the chromocentre of 3L beyond 80C; the complex translocation w^{258-36}, in which a heterochromatic piece of 2R, 41B to 41F5 is inserted between two euchromatic segments of *X* before 4C3–4; and several other aberrations in which one break has occurred in an euchromatic and the other in a heterochromatic region, including $T(1;3)N^{264-70}$, $T(1;2;3)N^{264-74}$, $T(1;3)^{305-33}$ and $ln(1)^{313-25-36}$. Both the aceto-carmine and the Feulgen techniques have been used for staining. In this material, evidence of loss or change of euchromatic bands translocated to a heterochromatic region, or vice versa, has been found only in the case of $ln(1)^{313-25-36}$, where bands from 2B transposed to the chromocentre appear darker than the homologous bands in the normal *X* in ten out of twenty-eight nuclei observed. Bands from the white-facet region in 3C show no change when they are adjacent to heterochromatin.

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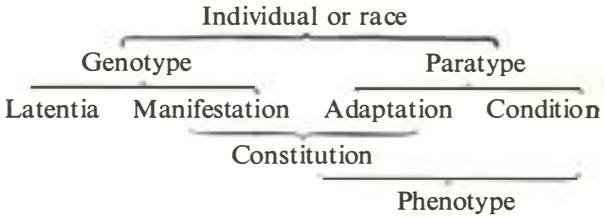
SZABÓ, Z. ***The Connexion between Genotype and Constitution***

The concept of constitution cannot be identified with that of genotype and of paratype or phenotype. I distinguish in both the genotype and the paratype two component elements. The suppressed-recessive and cryptomeric genes present in the genotype, as well as genes unable to become manifested owing to the absence of other conditioning genes (latentia), do not form a part of constitution, the latter including only the dominant, the double recessive allelomorphs, and the epistatic genes (manifestation). This manifested part represents the heritable component of constitution. Paratype includes in the first place those characters which influence the mode of reaction of the individual; many of them can be shown to take part in the control of development and activity of the individual, and throughout the life of the individual they affect permanent or at least durable and irreversible characters, i.e. they influence its adaptation. In contrast to these, there are transient, reversible changes which refer to only such modifications which do not form a part of constitution, but belong to the category of condition. The manifested genotype and the adapted paratype together form constitution, the latentia and condition do not. The phenotype is in the same relation to these conceptions as observableness is to non-observableness, i.e. it is the sum of only those characters which belong either to the manifested genotype or to the paratype, i.e.



The phenotype represents the object of observation and the latentia is dropped of itself. Experiment or medical intervention can easily detect the elements belonging to the category of modifiable and reversible condition. The individual always exists in some condition, therefore the definition of the phenotype refers only to a certain point of time and to a certain environmental complex. The constitution of the individual can be demonstrated after deducting the conditional symptoms. In the case of an individual, it cannot be determined whether the characters belonging to constitution be hereditary or acquired, but comparison, breeding, experiments and investigation of the family and of twins may throw light on this matter.

These statements refer to the analysis of the individual, but they may also successfully be employed for the race, and racial characters can be resolved into the same elements. The racial genotype contains the sum total of genes of all individuals comprising the race, but the environment produces the racial paratype. In the case of every true race it can be stated what constitution is represented by it under identical circumstances, i.e. what adaptation to the peristasis is developed by the genotype.

The appearance of the various constitutions is characteristic of the population, but even from this may be derived the fact that parallel constitutions are found in different races, because genotypes differing from one another may contain identical genes which produce identical characters.

The transformation of races (acclimatization) and the origin of new races may be largely attributed to the quantitative or qualitative, absolute or relative variation of the two components of the race constitution. Slight influences first change only the con-

dition of the race, deeper peristatic influences produce adaptational appearances which last, as long as the race lives in the same environment, but permanent modifications survive these influences and lead to mutations which transform the genotype of the race.

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TATUM, E.L., BEADLE, G.W. and CLANCY, C.W. ***Effect of Diet on Growth and Eye-colour Development in*** **Drosophila**

It is known that vermilion brown larvae, when placed on a low food-level diet, are capable of producing v^+ eye-colour hormone, and that they therefore develop pigmented eyes. This effect is associated with a prolongation of larval life during a specific developmental period. Prolongation of larval life by factors other than limited food intake does not appear to result in pigment production. Recent work of Khouvine, Ephrussi and Chevais has indicated that pigment production is inhibited when sugar is added to a low-level diet, but the possibility that the action of the sugar is upon yeast growth was not eliminated. We have studied the effects, under aseptic conditions, of various supplements to a low-level diet of dry yeast. The results indicate that carbohydrates and certain other substances suppress the so-called "starvation effect" and prevent pigment production, even though larval life is prolonged during the "sensitive" period. Glucose, sucrose, starch and alcohol, in a 2 % concentration, completely inhibit pigment production. Other substances which also inhibit pigmentation to a greater or lesser degree but which show definite toxicity for the larvae, are butter-fat, sodium acetate, sodium benzoate, and glycerol. Calcium lactate is non-toxic and has only a very slight inhibiting effect. In contrast to carbohydrates, which have a definite effect, proteins and amino acids, including hydrolysed casein and tryptophane, under aseptic conditions, have no significant effect on either duration of larval life or on pigment production. Some evidence, however, suggests that tryptophane may increase pigment production through the intermediation of growing micro-organisms. These results seem to show that a low carbohydrate level in the diet leads to production of v^+ hormone and eye pigment in suboptimally fed vermilion brown larvae.

The effect of low food level appears to be on the fat body. Fat bodies from both wild-type and "starved" vermilion brown larvae release v^+ hormone after transplantation into normal vermilion brown animals, while normal vermilion brown fat bodies do not. In addition, there is some evidence that there is an associated histological difference between wild-type and "starved" vermilion brown fat bodies, which are able to release the hormone, and normal vermilion brown fat bodies, which are unable to do so.

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TAVČAR, A. ***Inheritance of*** **2-, 3-, 4-** ***and*** **6-***articulate Leaf Whorls in* **Zea Mays** ***L.***

Maize has alternate leaves with a divergence of 1 : 2. Observations have been made on the progeny of a cross of two genotypes with normal phyllotaxis, which have been maintained for 6 years by selfing. In 1927, a decussate plant was found in the F_2. Since this phyllotaxis was at that time unknown, not only in maize but in monocotyledons in general, and since it proved to be hereditary, it was subjected to an exact genetical analysis, investigations extending over 11 years and comprising 106,450 plants. The results obtained were as follows. In typically decussate plants all leaves are cruciate-opposite. When such plants carry two ears, the two are usually opposite, but in plants with four or six ears, cruciate-opposite. The lower branches of the panicle are usually decussate. Selfing typically decussate plants during 10 years failed to produce constant decussate phyllotaxis, selfed decussate plants giving on the average 13·72 % of decussate plants, 0·57 % of 3-articulate, 0·06 % of 4-articulate, and 0·001 % of 6-articulate leaf whorls. In addition, there were some 6·06 % of transition types from normal to decussate and to 3- and 4-articulate leaf whorls. The height of the plants showed graduated decrease with the insertion of two to six leaves in one place. Selfed plants with 3-, 4- and 6-articulate leaf whorls gave rise to progeny which contained almost the same proportion of decussate plants and plants with 3-articulate whorls as those produced by the selfing of decussate plants, but none with 4- and 6-articulate. Crosses of decussate with normal plants gave in the F_1 8·14 % decussate and 0·23 % of 3-articulate whorls. Crosses of normal with 3-, 4-, and 6-articulate whorls gave, on the average, the same proportions of the various types as the crosses of normal with decussate. The F_1 from crosses of decussate plants, and of 3-, 4-, and 6-articulate whorls with normal showed a higher proportion of normal plants than the reciprocal cross. Plants with normal phyllotaxis produced only normals.

Ten plants were found in which the main stem carried decussate leaves, while the accessory ones had normal phyllotaxis. Further, there were two plants in which the main stem carried 3-articulate whorls and the accessory one, normal. Selfing of these two types produced in each case normal, decussate and 3-articulate plants. The main stem must

have a different genetic constitution from that of the accessory stems.

From all the above-mentioned crosses it follows that decussate plants, as well as the 3-, 4-, and 6-articulate ones, are produced by the mutation of one unstable gene. The genes for the different insertions are multiple alleles and mutate from one to the other. The following symbols are proposed: normal insertion *In*, decussate $In^{dec.}$, 3-articulate $In^{tr.}$, 4-articulate $In^{q.}$, and 6-articulate $In^{s.}$.

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Taylor, G.L. and Prior, Aileen M. ***The Distribution of the* M *and* N *Factors in Random Samples of Different Races***

Published data on the distribution of the *MN* blood groups in many parts of the world have been examined for agreement with the genetic theory of Landsteiner and Levine, and very considerable departures from expectation have been demonstrated. There is no reason at all to believe that these results throw any doubt on the accuracy of the theory, with which the data of a large number of experienced workers are in entire agreement. It seems almost certain that the discrepancies found are due to the use, by some workers, of faulty technique in the diagnosis of the *M* and *N* factors.

The proportions of *M* and *N* genes in the peoples of different nations have been examined, and although in certain nations there is great heterogeneity amongst the component sets of data, there is, after making allowance for such heterogeneity within nations, evidence of real heterogeneity between the nations.

The departure from expectation of the numbers of heterozygotes, *MN*, has also been examined, and heterogeneity of the data as a whole has been found, which heterogeneity must be due to errors in diagnosis if it is agreed that the genetic theory is correct, and if the populations examined were in genetic equilibrium. That there is no evidence of heterogeneity between the nations, after allowing for variation within nations, tends to confirm Landsteiner and Levine's theory of inheritance.

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Teodoreanu, N. ***Studies in Artificial Insemination of Sheep***

Injection of undiluted sperm immediately after collection (1–2 min.) to eighty-two ewes on heat resulted in 96·47 % of fertility, a figure which is equal to that obtained with normal mating and higher than that recorded by other authors. A dose of 0·1 c.c. is sufficient. In hand mating, some 4 % of the ewes fail to conceive. The percentage of twinning equalled 15·85, which resembles the figure obtained in hand mating in ewes under the same environmental and feeding conditions. The birth weight and vigour of lambs (male) is the same as with natural mating, viz. the birth weight of Merino lambs 5·63 kg., of Tzigai 4·35 kg., and of cross-bred 4·21 kg. Development and gain in weight are normal. On 1 April the weight of male lambs was as follows: Merino 10·27 kg., Tzigai 8·55 kg., and cross-bred 7·51 kg. On 1 May the respective figures were 17·25, 15·86 and 13·81 kg. The length of gestation in ewes which have been inseminated artificially is the same as in those which have mated normally. The results of all experiments on artificial insemination indicate that the percentage of fertilization is higher if undiluted sperm is used.

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Thomson, W.P. ***The Frequency of Fertilization and the Nature of Embryo and Endosperm Development in Intergeneric Crosses in Cereals***

By examination of ovaries fixed at various periods after a series of intergeneric pollinations in cereals, it was determined, (1) whether fertilization had occurred, (2) if so, the nature and extent of embryonic and endospermic development, and (3) the immediate cause of failure in those cases in which seeds were not formed. The crosses include *Hordeum* × *Secale*, *Triticum* × *Secale*, and *Triticum* × *Agropyron*. Several different combinations were used in each case. The results of one may be mentioned here: when a certain variety of barley is pollinated by rye, fertilization takes place in more than 90 % of the ovaries, embryos develop normally up to 4 days, but later die and by 8 days begin to disintegrate, numerous characteristically abnormal endosperm nuclei are produced but cells are never formed, and the endosperm always dies within a few days. The results of the other crosses are described. They include various conditions from complete failure of fertilization to almost completely successful seed production.

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Timoféeff-Ressovsky, N.W. ***Mechanismus der Punktmutationen***

1. Einleitung

Die Theorienbildung der experimentellen Genetik hat in erstaunlicher und bewundernswerter Weise ermöglicht, recht tief in den Aufbau des Genotyps hineinzublicken. Die vor einigen Jahren aufegebaut

Zytogenetik der Speicheldrüsenchromosome der Dipteren zeigte ein mikroskopisch sichtbares, sozusagen makrophysikalisches Bild, das den theoretisch entwickelten Vorstellungen über den Genotypenbau nicht nur im allgemeinen, sondern auch in vielen Einzelheiten entspricht. Einer tieferen direkten Analyse der Genbeschaffenheit sind aber doch zunächst schwerüberbrückbare Schranken gesetzt, indem: (1) wir nicht in der Lage sind, genügende Mengen der Substanz bestimmter Gene anzusammeln, um sie einer direkten Analyse unterziehen zu können, und (2) die wesentlichen Einheiten des Genotyps und deren struktureller Zusammenhang an sich in einer submikroskopischen, der makrophysikalischen Beobachtung und Analyse nicht zugänglichen Grössenordnung liegen. Wesentliche weitere Einblicke in die Natur der Gene sind deshalb wieder aus der theoretischen, auf indirekten experimentellen Angriffen aufbauenden Erforschung des Genproblems zu erwarten. Dabei kann es sich vor allem um zwei Arbeitsrichtungen handeln: (1) die Analyse der unmittelbaren Genwirkungen, und (2) die Analyse der Genänderungen.

Von Erkenntnissen, die zur Bildung allgemeinerer Theorien der unmittelbaren Genwirkung führen könnten, sind wir noch recht weit entfernt. Es gelingt noch nicht die Zelle zu "durchbrechen", und von Gesamtwirkungen genetisch bestimmt konstituierter Zellen (mögen sich diese Gesamtwirkungen auch unter Einfluss einzelner Genänderungen in bestimmter Weise ändern) zu den eigentlichen unmittelbaren Genprodukten vorzudringen. Vielleicht wird hier in Zukunft eine tiefere Analyse der Positionseffekte und der Genwirkungen innerhalb einzelner Zellen und einzelliger Organismen weiterführen.

Die Mutationen betreffen dagegen sicherlich unmittelbar das genische Substrat, den stofflichen Bau des Genotyps. Erkenntnisse des Wesens und der Gesetzmässigkeiten des Mutierens, müssen uns also wesentliche Aufschlüsse auch über die Natur der Gene ergeben. Dabei kann in der diesem Ziele dienenden Mutationsforschung entweder eine mehr "genetische" oder eine vorwiegend "biophysikalische" Methodik angewandt werden.

Hier möchte ich über die bisherigen Ergebnisse von biophysikalisch orientierten Arbeiten berichten, die die Klärung des Mechanismus des Mutationsvorganges zum Ziele hatten. Versuche über Auslösung von Mutationen durch ionisierende Strahlungen sind besonders geeignet um in erster Annäherung in das Wesen des Mechanismus des Mutationsvorganges einzudringen, da der einwirkende Faktor (die ionisierende Strahlung) und seine physikalische Wirkungsweise wohl-definierbar und weitgehend bekannt sind. Wir wollen deshalb zunächst die wichtigsten einschlägigen Ergebnisse der Strahlengenetik sichten, um dann eine theoretische Vorstellung über den Mechanismus des bei Bestrahlung stattfindenden Primärvorganges, der zur Entstehung von Punktmutationen führt, zu entwickeln, und schliesslich die entwickelte Vorstellung prüfen, eine ihr entsprechende Vorstellung über die Ursachen des spontanen Mutierens aufbauen und einige noch ungelöste Probleme und weitere Arbeitsrichtungen aufzählen.

2. Strahlengenetische Versuche

Wesentliche Aufschlüsse über den physikalischen Primärvorgang der Mutationsauslösung durch Strahlungen können aus Dosis-, Zeitfaktor- und Wellenlängenversuchen gewonnen werden. Das kann aber in sinnvoller Weise nur dann geschehen, wenn es sich herausstellt, dass dieser Primärvorgang mit genügender Wahrscheinlichkeit mehr oder minder direkt die Chromosomen selbst betrifft, und wenn die allgemeine Art der mutationsauslösenden Strahlenwirkung uns zeigt, dass Verallgemeinerungen der gewonnenen Ergebnisse als berechtigt erscheinen. Wir müssen deshalb zunächst das allgemeine Gesamtbild des strahleninduzierten Mutierens ins Gedächtnis zurückrufen.

(*a*) *Allgemeine Art der Strahlenwirkung.* Durch viele Versuche an verschiedenen Objekten wurde mit genügender Sicherheit bewiesen, dass die Bestrahlung einen ganz allgemeinen beschleunigenden Einfluss auf den Mutationsprozess ausübt, indem alle möglichen Typen von Mutationen durch Bestrahlung erzeugt werden können. Die Strahlenwirkung übt auch nicht nur zerstörende Wirkung auf die Gene aus, was unter anderen dadurch bewiesen wird, dass bei mehreren Allelenpaaren und innerhalb einiger multipler Allelenreihen Mutationen in verschiedenen, auch direkt

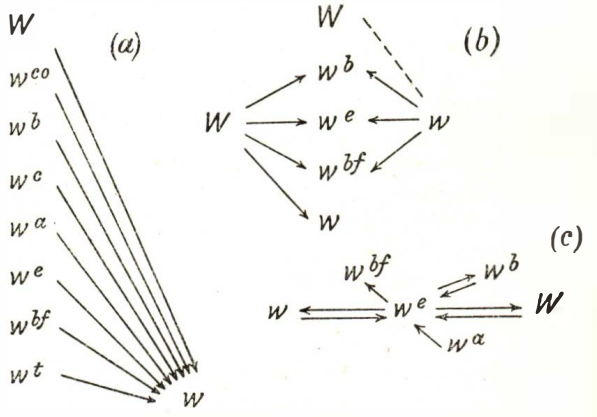

Abb. 1. Röntgeninduzierte Mutationen innerhalb der multiplen white-Allelenreihe von *Drosophila melanogaster*. (*a*) Das Allel white (*w*) konnte aus 8 verschiedenen anderen Allelen erzeugt werden; (*b*) aus Normal (*W*) und aus white (*w*) wurden die gleichen Allele blood (w^b), eosin (w^e) und buff (w^{bf}) erzeugt; (*c*) verschiedene Mutationsschritte die von und zu eosin erzeugt werden konnten. (Timoféeff-Ressovsky.)

entgegengesetzten Richtungen durch Bestrahlung erzeugt werden konnten (Abb. 1). Rückmutationen werden allerdings, wie auch die meisten bestimmten einzelnen Mutationsschritte (von einem bestimmten Allel zu einem anderen bestimmten Allel), in sehr geringer Rate erzeugt; es wurden aber einerseits innerhalb recht vieler verschiedener Allelenpaare Rückmutationen beobachtet (Tab. 1), andererseits konnte

Tabelle 1. *Rückmutationen rezessiver mutanter Allele von* Drosophila melanogaster, *erzeugt durch Röntgenbestrahlung in Versuchen von Timoféeff-Ressovsky* (5000 *r.*) *und von Johnston und Winchester* (3900 *r.*)

	Timoféeff-Ressovsky		Johnston und Winchester	
Bestrahlte Allele und ihre Loci	Zahl der Allele	Zahl der Mutationen	Zahl der Allele	Zahl der Mutationen
X-Chromosom:				
0 *y*	21 897	0	69 923	1
0 *sc*	17 676	3	101 042	5
1·5 *w*	71 231	3	—	—
1·5 w^e	89 583	5	—	—
1·5 w^a	—	—	69 302	0
5·5 *ec*	17 676	0	57 323	0
14 *cv*	16 460	2	—	—
20 *ct*	12 914	0	57 323	1
33 *v*	29 384	2	61 119	1
36 *m*	18 637	1	39 923	4
44 *g*	12 914	0	57 323	5
56 *f*	34 811	8	130 421	17
62 *car*	—	—	69 302	2
Z-Chromosom:				
0 *ru*	12 755	1	—	—
26 *h*	27 155	1	—	—
42 *th*	5 681	0	—	—
44 *st*	27 155	1	—	—
48 p^p	63 541	10	—	—
50 *cu*	5 681	0	—	—
59 *ss*	63 541	2	—	—
62 – *sr*	5 681	0	—	—
71 e^s	27 155	1	—	—
101 *ca*	5 681	0	—	—
Total	587 202	39 0·0066 %	713 001	36 0·0051 %
Unbestrahlte Kontrolle	152 352	0	700 000	0

auch gezeigt werden, dass die quantitativen Verhältnisse von Hin- und Rückmutationen in vielen Fällen sehr verschieden sein können, wobei manchmal Rückmutationen häufiger als Hinmutationen sind (Tab. 2). Eine Reihe von Versuchen, hauptsächlich an *Drosophila*, zeigte auch, dass man eine direkte Wirkung der Bestrahlung auf den Genotyp der bestrahlten Zellen annehmen muss. Dieser Punkt bedarf einer gewissen Erläuterung. *A priori* könnte man annehmen, dass die ausgelösten Mutationen insofern nur indirekt mit der vorangehenden Bestrahlung zusammenhängen, als letztere in dem Zell-

Tabelle 2. *Vergleich der Zahlen von Hin- und Rückmutationen innerhalb von vier verschiedenen Allelenpaaren bei* Drosophila melanogaster, *erzeugt durch Röntgenbestrahlung mit Dosen von* 5000–6000 *r.* (*Timoféeff-Ressovsky.*)

	Hinmutationen		Rückmutationen	
Allelenpaare	Zahl der Gameten	Zahl der Mutationen	Zahl der Gameten	Zahl der Mutationen
$W \rightleftharpoons w$	106 500	43	71 000	0
$W \rightleftharpoons w^e$	106 500	10	89 500	3
$F \rightleftharpoons f$	43 000	11	44 000	15
$P \rightleftharpoons p$	67 500	1	63 500	10

plasma, eventuell auch in anderen Zellen, Geweben, oder Organen in dem bestrahlten Organismus irgendwelche Veränderungen erzeugt, die dann als eigentlicher mutationsauslösender Faktor wirken. In diesem Fall könnte man weitgehende Nachwirkungen, Einfluss des bestrahlten Zytoplasmas auf die Mutabilität unbestrahlter Chromosome, und auch eine "somatische Induktion" in der Form erwarten, dass unbestrahlte Geschlechtszellen innerhalb bestrahlter Individuen ihre Mutationsrate erhöhen würden. Eine ganze Reihe von Versuchen zeigte, dass dieses nicht der Fall ist, und dass im Gegenteil angenommen werden muss, dass die mutationserzeugende Strahlenwirkung eine direkte ist (Tab. 3, 4). Dabei

Tabelle 3. *Raten geschlechtsgebundener Mutationen bei* Drosophila melanogaster *in*: (1) *unbestrahlten Kontrollkulturen*; (2) *eine Generation nach Bestrahlung mit* 3000–5000 *r. Röntgenstrahlen, in X-Chromosomen, die direkt nach Bestrahlung mutationsfrei waren*; (3) *nicht-bestrahlten X-Chromosomen der Spermien, die sich nach Befruchtung in röntgenbestrahlten* (3000 *r.*) *Eiern befanden*; (4) *direkt nicht bestrahlten X-Chromosomen, die sich aber in ♂♂ befanden, die mit einer sehr hohen Dosis sehr weicher bis in die Gonaden nicht durchdringender Grenzstrahlen* (2·5 *kV.*) *bestrahlt wurden*; (5) *X-Chromosomen direkt nach Röntgenbestrahlung mit* 3000 *r.* (*Timoféeff-Ressovsky.*)

Versuche	Zahl der Chromosomen	Zahl der Mutationen	Prozent der Mutationen
Unbestrahlte Kontrollen	3708	7	0·19±0·07
Früher bestrahlte *X*-Chromosome	1839	4	0·22±0·10
Unbestrahlte *X*-Chromosome in bestrahlten Eiern	2163	3	0·14±0·07
P-♂♂ bestrahlt mit sehr weichen Röntgenstrahlen	945	3	0·32±0·18
X-Chromosome direkt mit 3000 r. röntgenbestrahlt	2239	198	8·84±0·59

Tabelle 4. *Zahl von "Mosaikmutationen" mit mutantem Fleck, der mehr als ein Drittel, oder weniger als ein Drittel des Körpers einnimmt, entstanden in Spermien von* Drosophila melanogaster: (1) *bei* ♂♂, *die am* 1.–5. *Tag nach dem Schlüpfen aus den Puppen röntgenbestrahlt* (4500 *r.*) *und sofort mit* $\widehat{XXY}$-♀♀ *gekreuzt wurden*; (2) *bei ebenso bestrahlten, aber erst zwei Wochen nach Bestrahlung mit* $\widehat{XXY}$-♀♀ *gekreuzten* ♂♂; (3) *bei* ♂♂, *die am* 15.–20. *Tag nach dem Schlüpfen bestrahlt* (4500 *r.*) *und sofort mit* $\widehat{XXY}$-♀♀ *gekreuzt wurden*; (4) *bei allen bestrahlten* ♂♂; *und* (5) *in unbestrahlter Kontrolle.* (*Timoféeff-Ressovsky.*)

Versuche	Zahl der F_1-♂♂	Zahl der Mosaiks mit einem mutanten Fleck: Grösser als 1/3 des Körpers	Kleiner als 1/3 des Körpers	Total	Prozentsatz der Mosaikmutationen
P-♂♂ im Alter von 1–5 Tagen bestrahlt (4500 r.) und sofort mit $\widehat{XXY}$-♀♀ gekreuzt	20 874	17	3	20	0·09 ±0·02
P-♂♂ im Alter von 1–5 Tagen bestrahlt (4500 r.) und 14 Tage danach mit $\widehat{XXY}$-♀♀ gekreuzt	14 368	13	—	13	0·08 ±0·02
P-♂♂ im Alter von 15–20 Tagen bestrahlt (4500 r.) und sofort mit $\widehat{XXY}$-♀♀ gepaart	13 483	17	1	18	0·13 ±0·03
Total bestrahlt	48 725	47	4	51	0·10 ±0·01
Unbestrahlte Kontrolle	16 732	—	—	—	—

muss unter "direkter" Wirkung die Absorption eines oder mehrerer Strahlenquanten bzw. der durch sie, oder schnelle Korpuskularstrahlungen, sekundär erzeugten Ionisationen im Gen oder seiner unmittelbaren molekularen Umgebung verstanden werden, die eine unmittelbare, zur Genänderung bzw. Mutation führende Reaktion oder Reaktionskette auslöst.

Das vorhin skizzierte Gesamtbild der allgemeinen Art der mutationsauslösenden Strahlenwirkung gestattet somit eine tiefere Analyse des strahleninduzierten Mutationsmechanismus, was selbstverständlich sehr wenig aussichtsreich wäre, falls diese Strahlenwirkung eine nur indirekte wäre. Hinzu kommt, dass unter quantitativ definierbaren, konstanten Bestrahlungsbedingungen die erzeugten Mutationsraten sehr konstant sind. Es ist zwar in einigen Versuchen gelungen, durch das Variieren einiger Nebenfaktoren (wie gleichzeitige chemische Behandlung, oder Benutzung verschiedener Gewebe und Entwicklungsstadien der zu bestrahlenden Organismen) die durch eine bestimmte Strahlendosis ausgelöste Mutationsrate zu variieren; der Einfluss dieser Nebenfaktoren bewegt sich aber immer innerhalb einer Grössenordnung und meistens geht er nicht über eine Verdoppelung der strahleninduzierten Mutationsrate hinaus, wogegen der Strahleneinfluss auf die Mutationsrate innerhalb von 2–3 und sogar 4 Grössenordnungen liegen kann. Für quantitativ genau auswertbare Versuche müssen aber danach nicht nur die Bestrahlungsbedingungen (ausser dem zu untersuchenden Faktor), sondern auch das bestrahlte Material und möglichst alle Nebenbedingungen konstant gehalten werden.

(*b*) *Dosis-, Zeitfaktor- und Wellenlängenversuche.* Wird die Dosis der Bestrahlung variiert, so steigt selbstverständlich mit Erhöhung der Dosis die Rate der erzeugten Mutationen. Es ist aber wichtig die Art der Dosisproportionalität der strahleninduzierten Mutationsraten genau zu bestimmen. Abb. 2

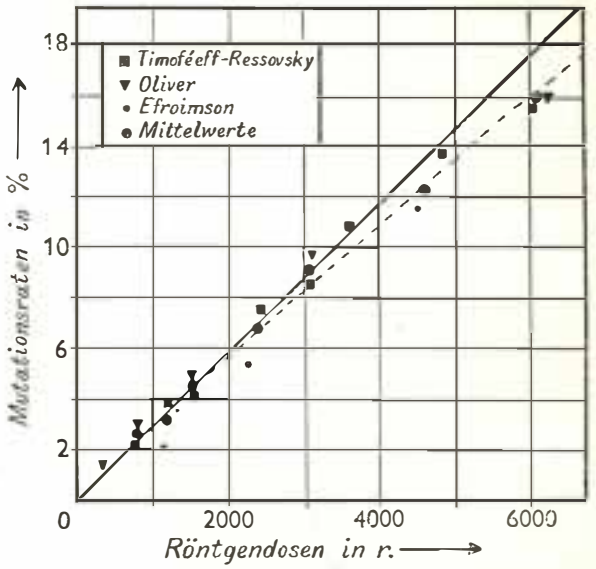

Abb. 2. Direkte Proportionalität der Raten geschlechtsgebundener Mutationen (hauptsächlich Letalfaktoren) zu den Röntgenbestrahlungsdosen (in r.-Einheiten) in "*CIB*"-Versuchen von drei verschiedenen Autoren bei *Drosophila melanogaster*.

zeigt die Versuchsergebnisse von drei verschiedenen Autoren an *Drosophila melanogaster*, aus denen hervorgeht, dass die Rate der geschlechtsgebundenen

Mutationen eine direkte Proportionalität zur Röntgenbestrahlungsdosis aufweist. Unter den in diesen Versuchen registrierten Mutationen sind sicherlich auch Chromosomenmutationen mit dabei; wie Abb. 3 zeigt gilt aber dieselbe direkte Dosisproportionalität auch für einzelne sichtbare Punktmutationen und für Gruppen bestimmter Punktmutationen bei *Drosophila*. Ähnliche direkte Dosisproportionalität der durch Röntgen- oder Radiumbestrahlung ausgelösten Mutationsraten wurde nicht nur bei *Drosophila*, sondern auch bei einigen anderen diesbezüglich untersuchten Objekten gefunden. Man kann somit behaupten, dass die Raten der Punktmutationen eine direkte Proportionalität zu den Bestrahlungsdosen aufweisen. Zieht man von den durch Bestrahlung erzeugten Mutationsraten die spontane Mutationsrate ab, so trifft die Dosisproportionalitätskurve mit genügender Sicherheit den Nullpunkt des Koordinatensystems. Schon daraus muss geschlossen werden, dass auch kleinste Dosen wirksam sein müssen und dass bei Summierung kleiner Dosen die Mutationsrate einfach der Summe der Einzelraten gleich sein muss. Es wurden aber auch spezielle Zeitfaktorversuche durchgeführt, in denen die zu verabreichenden Röntgenstrahlen- oder Radiumdosen fraktioniert, verdünnt, oder fraktioniert und verdünnt wurden. In verschiedenen Versuchsserien verschiedener Autoren wurde die Expositionsdauer von unter einer Minute bis zu über 500 Stunden variiert; wie aus Abb. 4 zu ersehen ist, konnte kein Einfluss des Zeitfaktors festgestellt werden. Es ist somit gleichgültig ob man die Bestrahlung verdünnt oder fraktioniert, es kommt bei der Auslösung von Punktmutationen lediglich auf die verabreichte Gesamtdosis an.

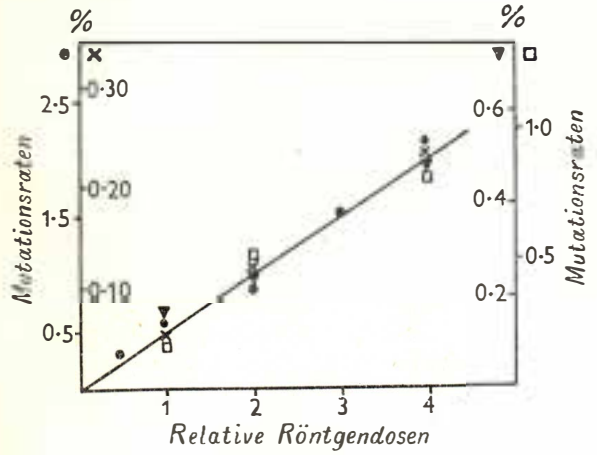

Abb. 3. Direkte Proportionalität der Raten sichtbarer (nicht-letaler) geschlechtsgebundener Mutationen zu den Röntgenbestrahlungsdosen bei *Drosophila melanogaster*. ●, somatische $w^e \rightarrow w$ Mutationen; ×, Summe von *y*, *w*, w^e, *v*, *m*, *g* und *f* Mutationen; ▼, alle sichtbaren Mutationen aus "$\widehat{XXY}$"-Versuchen; □, alle sichtbaren Mutationen aus "*ClB*"-Versuchen. (Timoféeff-Ressovsky und Delbrück.)

In verschiedenen strahlengenetischen Versuchen haben sich verschiedenste Strahlen, vom Ultraviolett über weiche und harte Röntgenstrahlen bis zu den härtesten Gammastrahlen des Radiums, schnelle Elektronen (Beta- und Kathodenstrahlen) und ionisierende Korpuskularstrahlungen (Rückstossprotonen und α-Teilchen) als wirksam im Sinne der Mutationsauslösung gezeigt. Für verschieden harte Röntgenstrahlen, Gammastrahlen und Betastrahlen stösst eine vergleichbare Dosierung, d.h. die Bestimmung äquivalenter, in Bezug auf Ionisationsraten gleicher Dosen, auf keine Schwierigkeiten. Es konnte deshalb die Wirksamkeit verschiedener Wellenlängen im Bereiche der Röntgen- und Gammastrahlung und die Wirksamkeit der Betastrahlung quantitativ verglichen werden. Auf Abb. 5 sind die Ergebnisse von genau dosierten Wellenlängenversuchen an *Drosophila melanogaster* angeführt; sie zeigen, dass im Bereich von Betastrahlen des Radiums und ganz weichen Röntgenstrahlen (sogen. Grenzstrahlen), über mittelharte Röntgenstrahlen, bis zu

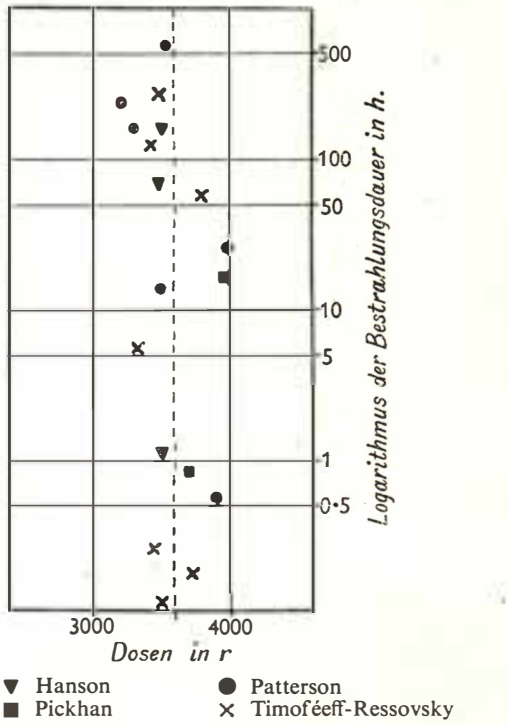

Abb. 4. Unabhängigkeit der durch Röntgen- und Radiumbestrahlung ausgelösten Mutationsraten vom Zeitfaktor (Intensität der Bestrahlung) bei *Drosophila melanogaster*. Die Ordinaten geben den Logarithmus der Bestrahlungszeit in Stunden an; die Abszisse — die Dosis die 10 % Mutationen erzeugt.

ganz harten Gammastrahlen des Radiums die mutationsauslösende Wirkung wellenlängenunabhängig ist und dass die ausgelösten Mutationsraten lediglich den in r.-Einheiten gemessenen Dosen proportional sind.

Die wesentlichsten Versuchsergebnisse über Auslösung von Mutationen durch Bestrahlung können somit folgendermassen zusammengefasst werden:

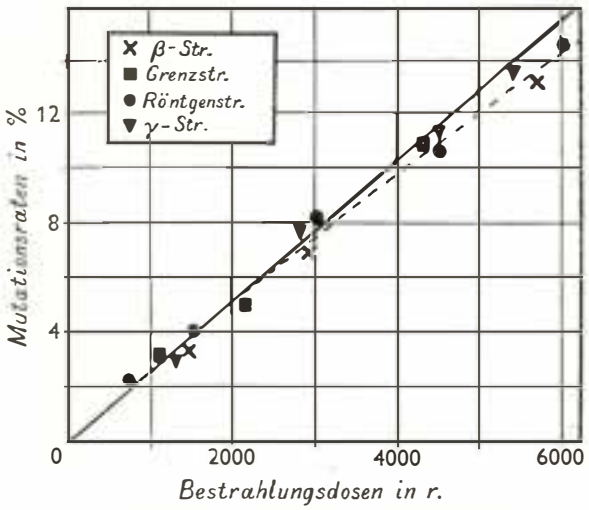

Abb. 5. Auslösung geschlechtsgebundener Mutationen bei *Drosophila melanogaster* durch: β-Strahlen des Ra, Grenzstrahlen (10 kV.), mittlere Röntgenstrahlen (100 kV.) und γ-Strahlen des Ra. (Timoféeff-Ressovsky und Zimmer.)

(1) die Bestrahlung übt einen im vorhin definierten Sinne direkten Einfluss auf die Chromosome aus, (2) die ausgelösten Mutationsraten sind den Bestrahlungsdosen direkt proportional, (3) es konnte kein Einfluss des Zeitfaktors, und (4) kein Einfluss der Wellenlänge der ionisierenden Strahlungen festgestellt werden.

3. Theorie des strahleninduzierten Mutationsvorgangs

Man kann jetzt versuchen, ausgehend von den Versuchsergebnissen der Strahlengenetik, sich eine Vorstellung über den physikalischen Primärvorgang bei der Strahlenauslösung von Mutationen zu bilden.

Bei biologischen Reaktionen, die auf direkter Einwirkung der Bestrahlung beruhen, kann das "Trefferprinzip" angewandt werden. Ionisierende kurzwellige Strahlen, Elektronen- und Korpuskularstrahlungen geben ihre Energie an den durchstrahlten Stoff in diskontinuierlicher Weise ab. Schematisch, in grober Annäherung, ist die Art dieser Energieabgabe auf Abb. 6 dargestellt. Die eingestrahlten Quanten lösen schnelle Sekundärelektronen aus, die längs ihrer Bahn weitere Ionisationen und Anregungen von Atomen erzeugen, bis ihre Energie dadurch aufgebraucht wird. Wesentlich für unsere weiteren Betrachtungen sind dabei folgende Tatsachen: die Quanten der kurzwelligeren Strahlungen sind energiereicher, lösen deshalb Sekundärelektronen von einer grösseren Reichweite aus, und diese Sekundärelektronen erzeugen, entsprechend ihrer höheren Energie, mehr Ionisationen und Anregungen von

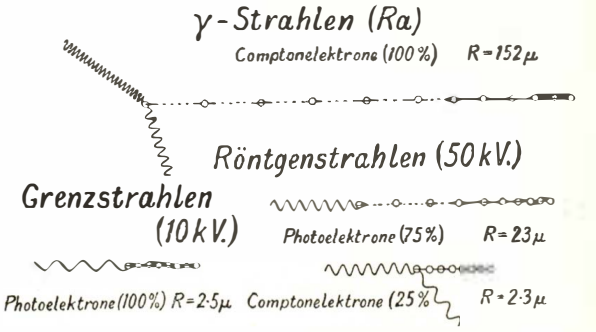

Abb. 6. Schematische Darstellung der Elementarvorgänge bei der Absorption der Energie der Quanten von ionisierenden Strahlungen im leichtatomigen durchstrahlten Stoff. R = mittlere Reichweite der Sekundärelektronen; ⊖ = Ionisationen der Atome; ○ = Atomanregungen. (Timoféeff-Ressovsky und Zimmer.)

Atomen längs ihrer Bahn; langwelligere Strahlen haben energieärmere Quanten, kürzere Reichweiten der Sekundärelektronen, geringere Zahlen von Ionisationen und Anregungen pro Sekundärelektron, aber wesentlich höhere Ionisationsdichte längs der Bahn des Sekundärelektrons. Da die Energieabgabe der ionisierenden Strahlungen in dieser diskontinuierlichen Weise erfolgt, so kann man die Bestrahlung gewissermassen mit einer Beschiessung vergleichen und, wenn man wohl-definierte Einheiten der biologischen Reaktion hat (wie es in ausgezeichneter Form bei der Mutationsauslösung gegeben ist), die Frage stellen, wieviel und welcher Art Treffer man für die Auslösung einer Reaktionseinheit benötigt. Für die Mutationsauslösung würde die Fragestellung also lauten: wieviele und welche von den diskontinuierlichen physikalischen Vorgängen der Energieabgabe im durchstrahlten Stoff zur Auslösung einer Mutation führen.

Die Frage über die Zahl der Treffer lässt sich durch Versuche über die Dosisproportionalität der Mutationsraten lösen. Auf Tab. 5 sind die Formalen angeführt auf Grund deren die Trefferzahl zu errechnen ist. Aus dieser Tabelle ist zu ersehen, dass bei direkter Dosisproportionalität, wie sie für die strahlenausgelösten Mutationsraten gefunden wurde, nur ein Treffer pro Mutation in Frage kommt.

Als Treffer können aber *a priori* dreierlei verschiedene physikalische Ereignisse in Betracht gezogen

Tabelle 5.

Die allgemeine Formel der "Schädigungskurve" ist

$$x = a\left[1 - e^{-kD}\left(1 + kD + \frac{(kD)^2}{2!} + \frac{(kD)^3}{3!} + \ldots + \frac{(kD)^{n-1}}{n-1!}\right)\right],$$

wobei

x = Anzahl der mutierten Gene,
a = Anzahl der bestrahlten Gene,
D = Strahlendosis,
k = Geschwindigkeitskonstante,
e = Basis der natürlichen Logarithmen,
n = Zahl der zur Schädigung eines empfindlichen Bereiches nötigen Treffer ist.

Die spezielle Formel für die Beziehung zwischen Mutationsrate und Strahlendosis ist

$$x = a(1 - e^{-kD}).$$

Die erste Formel geht in die zweite bei $n = 1$ über.

werden, was schematisch auf Abb. 7 dargestellt ist: entweder ist es die Absorption der gesamten Energie eines Quants, oder mehrere Ionisationen, die im

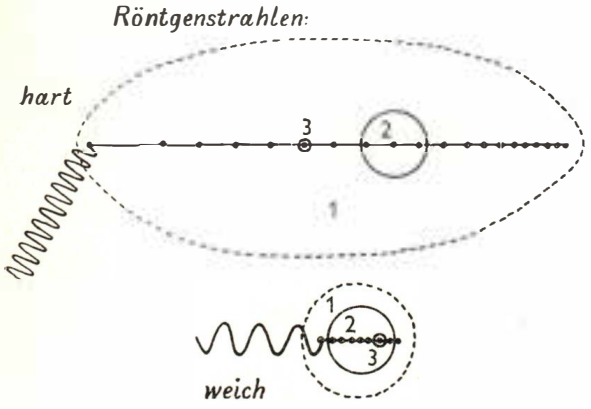

Abb. 7. Schematische Darstellung von drei denkbaren Annahmen über die Art des "Treffers": (1) Der Treffer besteht in der Absorption der gesamten Energie eines Quants; (2) Der Treffer besteht in dem Durchdringen eines bestimmten Volumens von einem Sekundärelektron (wobei letzteres in diesem Volumen die Energie mehrerer Ionisationen hinterlässt); (3) Der Treffer besteht in einer einzigen Ionisation (bzw. Atomanregung). (Timoféeff-Ressovsky.)

reagierenden Volumen bei dessen Durchquerung von einem oder mehreren Sekundärelektronen hinterlassen wurden, oder schliesslich eine einzelne Ionisation bzw. Anregung eines Atoms. Die Frage nach der Art des Treffers lässt sich auf Grund von Wellenlängenversuchen lösen. Tatsächlich, sollte die Absorption der Gesamtenergie eines Quants als Treffer gelten, so müssten harte Strahlen viel weniger wirksam als weichere Strahlen sein, da bei gleicher, in r.-Einheiten (also Ionisationsraten) gemessenen Dosis, man bei harter Strahlung wesentlich weniger Quanten hat als bei weicher Strahlung. Sind mehrere Ionisationen als Treffer zu betrachten, so muss sich wiederum ein Unterschied in der Wirkung verschiedener Wellenlängen ergeben. Denn es sind dann zweierlei Möglichkeiten denkbar. Entweder erfordert die Einleitung der Reaktionseinheit recht viel Energie, also recht viele Ionisationen; dann wird bei Anwendung langwelliger Strahlung, wegen der höheren Ionisationsdichte längs der Bahnen der Sekundärelektrone, eine geringere Trefferzahl pro Reaktionseinheit erforderlich sein (was sich in der Form der Proportionalitätskurve ausdrücken wird). Ist dagegen eine geringere Energiemenge, also wenige Ionisationen erforderlich, so wird harte Strahlung wirksamer als weichere sein, da bei Anwendung letzterer (wiederum wegen der höheren Ionisationsdichte längs der Bahnen der Sekundärelektronen) viele in das reagierende Volumen eintreffende Ionisationen überflüssig sein werden und sozusagen nutzlos verloren gehen würden. Nur bei der dritten Annahme, nähmlich dass als Treffer eine Ionisation (oder ein eng zusammenhängendes Ionenhäufchen) gilt, ist keinerlei Einfluss der Wellenlänge, weder auf die Wirksamkeit noch auf die Form der Dosisproportionalitätskurve, zu erwarten. In vereinfachter Form kann die vorhergehende Überlegung so ausgedrückt werden, dass falls die betreffende Reaktion einzig und allein der in r.-Einheiten gemessenen Dosis proportional ist, nur eine einzelne Ionisation als Treffer in Frage kommt.

Da, wie wir vorhin gesehen haben (Abb. 5), die ausgelösten Mutationsraten wellenlängenunabhängig sind, so muss angenommen werden, dass bei der Mutationsauslösung eine Ionisation als Treffer gilt; und da zur Auslösung einer Mutation nur ein Treffer erforderlich ist, so muss behauptet werden, dass eine Mutation durch eine Ionisation, bzw. Anregung eines Atoms ausgelöst wird.

Man muss sich also vorstellen, dass der Mutation die Absorption der Energie einer Ionisation innerhalb eines verhältnismässig sehr kleinen Volumens, das man als "Treffbereich" bezeichnen kann, zugrunde liegt. Kennt man die ungefähre Zahl der Atome pro cm.^{3} des organischen Stoffes, die Zahl der Ionisationen die in diesem Stoff durch eine r.-Einheit erzeugt werden und die Wahrscheinlichkeit der Erzeugung bestimmter wohl-definierter Mutationsschritte durch Bestrahlung mit 1 r. (die man als "Mutationskonstante" α bezeichenen kann), so kann man eine formale Grösse des Treffbereiches für diese Mutationsschritte, ausgedrückt in Zahl der Atome, berechnen. Für einige wenige einzelne Mutationsschritte ist ihre Beziehung zur Bestrahlungsdosis einigermassen bekannt, und auf Tab. 6 sind für diese Mutationsschritte die Mutationskonstanten α und die Treffbereiche a angeführt; letztere bewegen sich in den Grössen von 75–1650 Atome. Es muss aber dabei zweierlei betont werden. Erstens darf man

Tabelle 6. "*Mutationskonstanten*" (α = *Wahrscheinlichkeit des Mutierens nach Bestrahlung mit* 1 *r.*) *und* "*Treffbereiche*" (a = *Zahl der Atome, von denen eines getroffen werden muss um mit hoher Wahrscheinlichkeit die Mutation zu erzeugen*) *einiger Mutationsschritte bei* Drosophila melanogaster.

Die entspr. Formeln sind:

$$\alpha = \frac{\Sigma n_1}{\Sigma R_1 \times \Sigma N_1};\ a = 2{\cdot}5 \times 10^{10}\alpha.$$

(*Timoféeff-Ressovsky und Delbrück.*)

Mutationen	Mutationskonstanten α	Treffbereiche a
$W \rightarrow W^e$	$2{\cdot}6 \times 10^{-8}$	650
$w \rightarrow w^e$	$0{\cdot}3 \times 10^{-8}$	75
$w^e \rightarrow w$	$0{\cdot}8 \times 10^{-8}$	200
$M \rightarrow m$	$2{\cdot}4 \times 10^{-8}$	600
$m \rightarrow M$	$1{\cdot}0 \times 10^{-8}$	100
$F \rightarrow f$	$6{\cdot}6 \times 10^{-8}$	1650
$f \rightarrow F$	$2{\cdot}4 \times 10^{-8}$	600

nicht ohne weiteres die Grösse dieser Treffbereiche mit der Gengrösse in Zusammenhang bringen, denn die Treffbereiche sind definitionsgemäss lediglich das Volumen, innerhalb dessen die Energie des Treffers absorbiert werden muss, um mit grosser Wahrscheinlichkeit die in Frage kommende Mutation auslösen zu können; der Treffbereich kann danach grösser oder auch kleiner als die reagierende Einheit, also das Gen sein. Zweitens muss betont werden, dass die so berechneten Treffbereiche als minimale zu gelten haben, da sie auf Grund der Annahme einer absoluten Ionenausbeute berechnet werden; aus der Photochemie wissen wir aber, dass durchaus nicht alle Reaktionen eine absolute Ionenausbeute zeigen und die tatsächliche Ionenausbeute ist für die Mutationsauslösung uns nicht bekannt; da man aber mit hoher Wahrscheinlichkeit annehmen kann, dass in diesem Fall die Ionenausbeute geringer als 100 % ist, so müssen die realen Treffbereiche grösser als die vorhin berechneten sein.

Der physikalische Vorgang, der zur Auslösung einer Mutation durch ionisierende Strahlung führt, besteht demnach darin, dass eine Ionisation bzw. Anregung eines Atoms, falls sie in einem bestimmten Treffbereich, der innerhalb der Grössenordnung organischer Moleküle sich befindet, erfolgt, die Mutation zu erzeugen imstande ist. Da wir aus der Photochemie wissen, dass normalerweise einzelne Ionisationen bzw. Anregungen von Atomen monomolekulare Reaktionen zustande bringen, so muss angenommen werden, dass eine strahlenausgelöste Punktmutation ebenfalls in der Strukturänderung einer physikochemischen Einheit besteht.

Die oben entwickelte Vorstellung kann als Arbeitshypothese dienen und weiteren experimentellen Prüfungen unterzogen werden. Ich möchte hier eine derartige Prüfung, die in letzter Zeit durchgeführt werden konnte, erwähnen. Auf Grund der vorhin entwickelten Vorstellung muss erwartet werden, dass, falls man Korpuskularstrahlungen anwendet (α-Strahlung oder Rückstossprotonen), die längs der Bahn des Partikels sehr dicht ionisieren, in die Treffbereiche zu viele Ionisationen hineingeraten und, da nur eine erforderlich ist, nutzlos verloren gehen; es muss somit gewissermassen ein "Sättigungseffekt" sich ergeben, der dazu führt, dass bei äquivalenten (in r.-Einheiten gemessen gleichen) Dosen diese dicht ionisierenden Korpuskularstrahlungen etwas geringere Mutationsraten als die Röntgenstrahlen erzeugen würden. Wegen der sehr starken Absorption im Gewebe konnten Versuche mit genügend genau vergleichbaren wirksamen Dosen mit α-Strahlung zunächst nicht durchgeführt werden; solche Versuche sind erst im Gange unter Benutzung der Methode der künstlichen Besamung von *Drosophila*, die es ermöglicht Spermien *in vitro* zu bestrahlen und somit die wirksame α-Strahlendosis genau zu bestimmen. Es konnten aber Neutronenbestrahlungsversuche durchgeführt werden, bei denen die durch Rückstossprotonen am Wirkungsort erzeugte Ionisation mit genügender Genauigkeit gemessen, und in r.-Einheiten ausgedrückt werden konnte. Auf Abb. 8

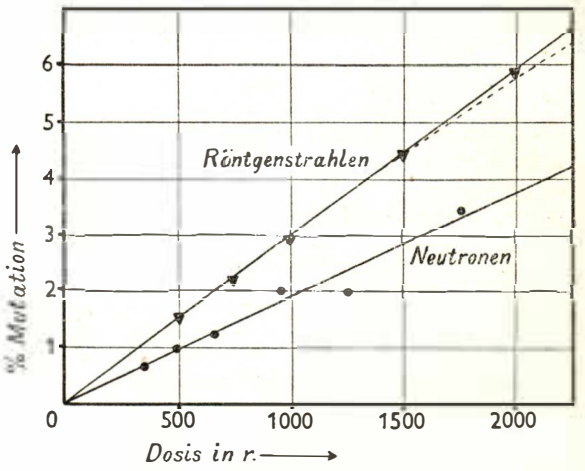

Abb. 8. Auslösung geschlechtsgebundener Mutationen bei *Drosophila melanogaster* durch äquivalente Dosen von Röntgen- und Neutronenbestrahlung. (Timoféeff-Ressovsky und Zimmer.)

ist das Ergebnis dieser Versuche dargestellt; sie zeigten, wie zu erwarten, dass die Neutronenbestrahlung um etwa 35 % bis 40 % weniger wirksam als die Röntgenbestrahlung ist und können somit als indirekte Bestätigung der vorhin entwickelten Vorstellung gedeutet werden.

4. Spontanes Mutieren

Die theoretische Auswertung der Versuche über Mutationsauslösung durch ionisierende Strahlungen führte zu der Vorstellung, dass der Mutationsmechanismus in einer durch eine Ionisation bzw. Anregung eines Atoms eingeleiteten Strukturänderung eines wohl-definierten Atomverbandes (einer physikochemischen Struktureinheit) besteht. Rein qualitativ sind viele Parallelen und Ähnlichkeiten zwischen dem strahleninduzierten und spontanen Mutieren, was die Punktmutationen betrifft, vorhanden; auf gewisse Unterschiede wird am Schluss noch speziell hingewiesen werden. Diese grosse Ähnlichkeit der beiden Mutationsprozesse zwingt zu der Annahme, dass auch bezüglich des Mutationsmechanismus eine gewisse Ähnlichkeit bestehen muss.

Tabelle 7. *Beispiel einer Schätzung der zur Erzeugung der spontanen Mutationsrate bei* Drosophila *nötigen Dosis der "natürlichen ionisierenden Strahlungen". (Timoféeff-Ressovsky.)*

m = Mutation; i = Ionisation;
$r.$ = Dosiseinheit der Röntgenstrahlung.

Wir nehmen an, dass:

(1) 3000 r. *ca.* 10 % geschlechtsgebundene Mutationen auslösen;
(2) die spontane Rate dieser Mutationen *ca.* 0·1 % ist;
(3) 1 r. erzeugt *ca.* 2×10^9 *i* pro cm.^{3};
(4) die natürlichen ionisierenden Strahlungen *ca.* 50 *i* pro sec. und cm.^{3} erzeugen;
(5) die Fliegen sind der "natürlichen Strahlung" während *ca.* 15 Tagen $= 1{\cdot}4 \times 10^6$ sec. exponiert;
(6) die Mutationsraten sind den Bestrahlungsdosen direkt proportional.

Somit ist:

$$\begin{array}{r} 3000\ \text{r.} - 10\ \%\ m \\ X\ \text{r.} - 0{\cdot}1\ \%\ m \end{array} \quad \text{oder} \quad \begin{array}{l} 10\ \%\ m - 6 \times 10^{12}\ i \\ 0{\cdot}1\ \%\ m - X\ i; \end{array}$$

es ergibt sich:

$X = \dfrac{6 \times 10^{12}}{100} = 6 \times 10^{10}\ i$ = der Dosis der "natürlichen Strahlungen", die erforderlich ist um die spontane Mutationsrate zu erzeugen.

Aber:

$50\ i \times 1{\cdot}4 \times 10^6 = 7 \times 10^7\ i$ = der tatsächlichen durchschnittlichen Dosis der "natürlichen Strahlungen", der die Fliegen im Freien oder im Laboratorium ausgesetzt sind;

wir sehen also dass:

$\dfrac{6 \times 10^{10}}{7 \times 10^7} = 875$, oder dass die tatsächliche Intensität der "natürlichen ionisierenden Strahlungen" *ca.* 875 mal zu schwach ist, um für die gesamte Höhe der spontanen Mutationsrate von *Drosophila* verantwortlich gemacht zu werden.

Kurz nach Entdeckung der mutationsauslösenden Wirkung der Röntgenstrahlen wurde von verschiedenen Seiten die Vermutung ausgesprochen, dass die spontane Mutabilität eventuell auf die "natürliche ionisierende Strahlung" (die sich aus kosmischer Strahlung und, zu einem kleinen Teil, aus der Radioaktivität der Erde zusammensetzt) zurückgeführt werden könnte. Berechnungen verschiedener Autoren haben aber bald gezeigt, dass die natürliche ionisierende Strahlung viel zu schwach ist, um für die Rate der spontanen Mutationen verantwortlich gemacht zu werden; auf Tab. 7 ist ein Beispiel einer Berechnung zur Prüfung dieser Frage angeführt. Ein anderer Weg die Frage über die Bedeutung der natürlichen ionisierenden Strahlung für die spontane Mutabilität zu prüfen besteht in dem Variieren der Intensität der Höhenstrahlung, entweder durch Änderung der Höhenlage, oder durch Verwendung verschieden dicker Bleifilter; in letzterem Fall kann eine bestimmte Dicke der Bleischicht gewählt werden, unter der die grösste, durch sogenannte "Schauerbildung" der Höhenstrahlen erzeugte Ionisation herrscht. Ist die kosmische Strahlung für die spontane Mutabilität von Bedeutung, so müssen sich wesentliche Änderungen der durch sie erzeugten Ionisation in entsprechenden Änderungen der spontanen Mutationsraten ausdrücken. Auf Tab. 8 sind

Tabelle 8. *Versuche über einen event. Einfluss der kosmischen Strahlung auf die Rate spontaner geschlechtsgebundener Mutationen bei* Drosophila melanogaster. *P-♂♂ wurden (vor der Kreuzung mit "ClB"-♀♀) 20 Tage lang gehalten in: (a) Holzkästchen (Kontrolle), (b) Kästchen mit 15 mm. Bleipanzerung, oder (c) Kästchen mit 50 mm. Bleipanzerung. In (b) war die durch kosmische Strahlung erzeugte Ionisation wesentlich höher als in (a) und (c). (Timoféeff-Ressovsky und Rajewsky.)*

Bedingungen	Zahl der Gameten	Zahl der Mutationen	Prozentsatz der Mutationen
(*a*) Kontrolle	6467	18	0·288 ±0·067
(*b*) 15 mm. Blei	6594	18	0·273 ±0·064
(*c*) 50 mm. Blei	6235	17	0·272 ±0·066

derartige Versuche angeführt, deren Ergebnisse im Einklang mit den Berechnungen der Tab. 7 vollkommen negativ ausgefallen sind. Es muss also angenommen werden, dass die natürliche ionisierende Strahlung nur einen verschwindend geringen Teil der spontanen Mutationen erzeugt, und es muss nach anderen Erklärungen für das spontane Mutieren gesucht werden.

Die physikalische Chemie lehrt uns, dass monomolekulare Reaktionen, also Strukturänderungen wohl-definierter Atomverbände, nicht nur durch Energiezufuhr von aussen (in Form von Ionisationen

bzw. Anregungen von Atomen durch Strahlung, Punktwärme oder chemische Beeinflussung) zustande kommen können, sondern auch durch Lösung von Bindungen innerhalb des Atomverbandes, bedingt durch überschwellige Temperaturschwankungen der Atome gegeneinander; das sind die "spontanen monomolekularen Reaktionen", die für verschiedene Atomverbände verschieden schnell verlaufen (also verschiedene Halbwertszeiten haben) und deren Geschwindigkeit von der Höhe der Bindungsenergie bzw. Aktivierungsenergie abhängig ist. Man könnte annehmen, dass ein wesentlicher Teil der spontanen Mutationen auf diesem Wege zustande kommen. Dann müsste aber die spontane Mutationsrate den reaktionskinetischen Grundregeln folgen, nämlich Zeitproportional und temperaturabhängig sein. Denn monomolekulare Reaktionen sind zeitproportional und zwischen Aktivierungsenergie, Halbwertszeit und dem Temperaturkoeffizienten der betreffenden Reaktion besteht ein Verhältnis, dass in gewisser Annäherung auf Tab. 9 dargestellt ist; wesentlich ist

Tabelle 9. *Beziehungen zwischen der Aktivierungsenergie einer Reaktion, ihrer Geschwindigkeit und ihrem Temperaturkoeffizienten.* (*Timoféeff-Ressovsky, Zimmer und Delbrück.*)

Aktivierungsenergie in eV	Reaktionsgeschwindigkeit in $1/W$	Temperaturkoeffizient $t^{\circ}Q_{10}$
0·3	2×10^{-10} sec.	1·4
0·6	5×10^{-6} sec.	1·9
0·9	0·1 sec.	2·7
1·2	33 min.	3·8
1·5	16 Monate	5·3
1·8	30 000 Jahre	7·4

dabei, dass stabile Reaktionen einen höheren Temperaturkoeffizienten als labilere aufweisen. Versuche an einigen pflanzlichen Objekten und an *Drosophila* zeigen, dass in ruhenden Zellstadien spontane Mutationen sich ungefähr zeitproportional anhäufen; auf Tab. 10 sind *Drosophila*-versuche angeführt, die

Tabelle 10. *Raten geschlechtsgebundener Mutationen in (a) frischen (sofort nach Schlüpfen) und (b) alten (20 Tage nach dem Schlüpfen) reifen Spermien der* Drosophila melanogaster *Männchen. "ClB"-Versuche, dauernd bei Zimmertemperatur* (21°–22° C.). *Zusammenfassung früherer* (1935) *und neuer Versuchsergebnisse.* (*Timoféeff-Ressovsky.*)

Alter der Spermien	Zahl der Kulturen	Zahl der Mutationen	Prozentsatz der Mutationen
(*a*) *P*-♂♂ sofort nach dem Schlüpfen gepaart	13 481	14	0·104 ±0·028
(*b*) *P*-♂♂ 20 Tage nach dem Schlüpfen gepaart	18 659	49	0·263 ±0·038

Differenz$_{1-2}$ = 0·159 ±0·047.

dieses zeigen. An *D. melanogaster* wurden auch von verschiedenen Autoren Versuche durchgeführt, aus denen klar hervorgeht, dass mit Erhöhung der Temperatur die spontane Mutationsrate ansteigt, mit einem Temperaturkoeffizienten von ungefähr

$$t^{\circ}Q_{10} = 5{\cdot}7 \text{ (Tab. 11).}$$

Tabelle 11. *Einfluss der Temperatur (innerhalb "normaler" physiologischer Grenzen) auf die Rate spontaner geschlechtsgebundener Mutationen bei* Drosophila melanogaster. (*Timoféeff-Ressovsky.*)

Temperatur	Zahl der Gameten	Zahl der Mutationen	Prozentsatz der Mutationen
P-♂♂ in 14° C.	10 417	9	0·086 ±0·029
P-♂♂ in 22° C.	7 841	15	0·191 ±0·051
P-♂♂ in 28° C.	8 936	31	0·347 ±0·063

Differenz:$_{1-3}$ = 0·26 ±0·07.

Dauer der Generation: 14° C., 22; 22° C., 14; und 28° C. 11 Tage; Korrigierte Mutationsraten: 0·055 %, 0·191 % und 0·441 %; Temperaturkoeffizienten: $t^{\circ}Q_{10} = 2{\cdot}9$; $t^{\circ}Q_{10\ \text{korrigiert}} = 5{\cdot}7$.

Es zeigt sich somit, dass die spontane Mutationsrate tatsächlich zeitproportional und temperaturabhängig ist, und einen Temperaturquotienten aufweist, der für langsame Reaktionen, also stabile Gebilde charakteristisch ist; und da die absolute Höhe der spontanen Mutationsraten gering ist, so geht daraus hervor, dass es sich um Änderungen von stabilen Gebilden handelt. Eine besondere Bestätigung findet diese Interprätation des spontanen Mutierens darin, dass, wie auf Grund der auf Tab. 9 wiedergegebenen reaktionskinetischen Gesetzmässigkeit zu erwarten ist, besonders häufige Mutationen einen niederigeren Temperaturkoeffizienten aufweisen; das zeigen die auf Tab. 12 angeführten Tem-

Tabelle 12. *Einfluss der Temperatur (innerhalb "normaler" physiologischer Grenzen) auf die Rate spontaner Rückmutationen eines relativ unstabilen mutanten bobbed-Allels bei* Drosophila funebris. (*Timoféeff-Ressovsky.*)

Temperatur	Zahl der Gameten	Zahl der Mutationen	Prozentsatz der Mutationen
P-♂♂ in 15–16° C.	283 082	20	0·0070
P-♂♂ in 25–26° C.	368 131	47	0·0128

Dauer der Generation: 15° C., 21; 25° C., 13 Tage; Korrigierte Mutationsraten: 0·0070 % und 0·0207 %; Temperaturkoeffizienten: $t^{\circ}Q_{10} = 1{\cdot}83$; $t^{\circ}Q_{\text{korrigiert}} = 3{\cdot}00$.

peraturversuche mit einer Rückmutation, deren spontane Mutationsrate wesentlich höher als die durchschnittliche Mutationsrate normaler Allele ist.

Die vorhin entwickelte Ansicht über den Mechanismus des spontanen Mutierens entspricht nicht nur im wesentlichen den experimentell gewonnenen Tat-

sachen, sondern hat auch den Vorteil, dass sie, physikalisch betrachtet, das strahleninduzierte und spontane Mutieren gewissermassen unter einen Hut bringt; dadurch stützen sich gegenseitig die im vorherigen Kapitel für die strahleninduzierten und in diesem Kapitel für spontane Mutationen entwickelten Anschauungen über den Mutationsmechanismus.

5. Schlussbemerkungen

Die vorhin entwickelten Ansichten über den Mutationsmechanismus sind streng präzisiert nur in Bezug auf das physikalische Primärereignis das zu der Auslösung einer Mutation führt; der weitere eigentliche Änderungsmechanismus der in Frage kommenden Stelle des Genoms wird zunächst nur ganz allgemein als Strukturänderung (in gewissen Fällen auch Zerstörung) eines wohl-definierten Atomverbandes angenommen. Aus diesen Ansichten ergeben sich einerseits gewisse Konsequenzen und Voraussagen bezüglich der Eigenschaften des Mutierens unter verschiedenen Bedingungen, und andererseits, in Zusammenhang damit, gewisse weitere Arbeitsaufgaben. Beides soll hier nur ganz kurz gestreift werden.

Eine ganz allgemeine Konsequenz ergibt sich zunächst für die Frage über die Genstruktur. Wenn eine Punktmutation in einer Strukturänderung eines wohl-definierten Atomverbandes besteht, so muss auch das Gen (das begrifflich unter anderen an die Punktmutation gebunden ist), oder zumindestens sein wesentlichster Teil, ein wohl-definierter Atomverband sein. Ob nun ein Gen ein weitgehend autonomes grosses organisches Molekül als Glied einer Kette derartiger aneinander gebundener Moleküle, ein in gewissem Sinne abgegrenzter Teil einer grossen Mizelle, die einem ganzen Chromosom entsprechen würde, oder selbst eine mehr oder weniger komplizierte Mizelle als Teil eines aus vielen aneinander geketteten Mizellen bestehenden Verbandes darstellt, kann und soll zunächst nicht entschieden werden. Dazu sind weitere zytogenetische, zellphysiologische und physikalische Versuche notwendig. Wesentliches können Elektronenbeugungsaufnahmen isolierter Chromosome ergeben.

Aus den vorhin entwickelten Anschauungen über den strahleninduzierten Mutationsmechanismus einerseits und den spontanen andererseits ergibt sich, dass gewisse qualitative Unterschiede zwischen dem strahleninduzierten und spontanen Mutationsprozess zu erwarten sind; sie würden darin bestehen, dass gewisse durch Bestrahlung ausgelöste Mutationsschritte spontan praktisch nie aufträten, und dass umgekehrt gewisse spontan auftretende Mutationsschritte nur unwesentlich durch Bestrahlung beschleunigt werden. Gewisse Andeutungen darauf zeigen schon die bisher an verschiedenen Objekten durchgeführten Versuche; geklärt kann aber dieses nur an Hand eines sehr umfangreichen statistischen Materials werden. Es ist weiter zu erwarten, dass sehr viele chemische Faktoren, falls sie in unmittelbare Nähe der Gene gebracht werden können, die Mutationsrate erhöhen müssen. Chemische Behandlung, ebenso wie Bestrahlung mit sichtbarem und ultraviolettem Licht, könnte in gewissem Grade selektiv die Mutabilität beeinflussen, indem bestimmte Mutationsschritte auf diesem Wege bevorzugt und andere garnicht ausgelöst werden. Die Prüfung dieser Frage steht ebenfalls noch aus; bisher ist es lediglich gelungen zu zeigen, dass chemische Faktoren und, in noch stärkerem Grade, das Ultraviolett die Mutationsraten überhaupt zu erhöhen imstande sind. Es ist schliesslich zu erwarten, dass einige Nebenbedingungen die Stärke der mutationsauslösenden Wirkung der Strahlung beeinflussen könnten, voraussichtlich über Beeinflussung der Grösse der Treffbereiche. Eine ganz spezielle konkrete Aufgabe besteht in der Messung der tatsächlichen reellen Treffbereiche; dieses kann auf Grund von Mutationsauslösungsversuchen mit verschiedenen sehr dicht ionisierenden Korpuskularstrahlungen (verschieden schnelle α-Teilchen und Rückstossprotonen) gemacht werden, obwohl es zunächst auf gewisse technische Schwierigkeiten stösst; auf Grund der Kenntnis reeller Treffbereiche könnte man dann die Ionenausbeute des Mutationsauslösungsvorganges berechnen. Chemische Mutationsauslösung, Versuche mit Ultravioletstrahlung und Röntgenbestrahlungsversuche unter verschiedenen äusseren und physiologischen Bedingungen könnten weitere Aufklärung über die Art der zur Mutation führenden Reaktionen oder Reaktionsketten ergeben. Gewisse Aussichten dafür bot die Angabe einiger Autoren über den Einfluss der Temperatur auf die durch gleichzeitige Röntgenbestrahlung ausgelöste Mutationsrate; genaue Versuche, die auf Tab. 13 angeführt sind, konnten aber leider das Grundphänomen selbst nicht bestätigen. In denselben Rahmen fallen auch Versuche über den Vergleich von Mutationsraten in homologen Gebieten innerhalb normaler Chromosomen und in der Nähe von Bruchstellen; es sind schon gewisse Andeutungen darauf vorhanden, dass es eine Art Positionseffekt auf die Mutationsrate geben kann.

Schliesslich muss betont werden, dass wesentliche Fortschritte unserer Kenntnisse durch Kooperation und Koordination der Versuchsergebnisse aus den Gebieten der allgemeinen Mutationsforschung, der Zytogenetik, der mikrochemischen Chromosomenanalyse und der modernen Virusforschung zu erwarten sind. Zunächst müssen wir uns mit dem, was experimentell erreicht werden konnte begnügen und allzu bodenloser Spekulationen enthalten.

Tabelle 13. *Erzeugung geschlechtsgebundener Mutationen bei* Drosophila melanogaster *durch gleiche Röntgendosen bei verschiedener Temperatur während (und kurz vor) der Bestrahlung. Die Mutationskonstanten α_k (für "kalt") und α_w (für "warm"), die die Raten der Mutation pro* 1 *r. Bestrahlung darstellen, wurden nach der Formel* $\alpha = \frac{\Sigma n_i}{\Sigma R_i \Sigma N_i}$ *berechnet.* (*Timoféeff-Ressovsky und Zimmer.*)

Versuche	Temperatur °C	Zahl der Gameten	Zahl der Mutationen	Prozentsatz der Mutationen
I. Dosis	10	802	76	9·2±1·0
3000 r.	35	736	60	8·2±1·0
II. Dosis	3	838	73	8·7±1·0
2750 r.	33	748	57	7·6±1·0
III. Dosis	3	983	81	8·2±0·8
2750 r.	33	897	77	8·6±0·9
IV. Dosis	7	976	25	2·5±0·5
1200 r.	32	921	29	3·1±0·6

Totale Mutationskonstanten: $\alpha_k = 2{\cdot}89 \times 10^{-5}$; $\alpha_w = 2{\cdot}84 \times 10^{-5}$.

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TINNEY, F.W. *Cytology of Apomictic Seed-development in* Poa pratensis *L.*

Cytological observations on *Poa pratensis* show, in the biotypes studied, that the single macrospore mother cell undergoes meiosis in the usual manner and forms haploid macrospores—usually only three in number, since frequently the second meiotic division of the micropylar cell is not completed. In all of the observed instances the macrospores so formed were found to disintegrate.

A separately differentiated vegetative cell of the nucellus, near the chalazal end of the macrospore mother cell, becomes the initial cell of the embryo sac. This cell differentiates simultaneously with the meiotic divisions of the macrospore mother cell, and it develops, without meiosis, into a typical 8-nucleate, 7-celled embryo sac. The egg develops parthenogenetically into an embryo, and frequently this development begins before the stigma of the ovary is receptive to pollen. Anthesis usually precedes endosperm development, but it has not been shown that the presence of pollen on the stigma is prerequisite to the inception of the endosperm. Pollen tubes are commonly found in the style but have never been observed in the embryo sac. Hence, while these facts indicate that pollination is unnecessary to embryo development, its necessity for, or influence on, endosperm development is unknown. From the foregoing discussion, we may expect daughter plants to possess the same complement of chromosomes as their maternal parent, and, consequently, to be of similar morphological type. With a few exceptions, these expectations have been verified by observations.

Two embryos are occasionally found in a single ovule, but each is enclosed in a separate embryo sac. Each of these embryo sacs appears to develop from an individual cell of the nucellus. There is no evidence to indicate that embryos arise by sporophytic budding from the nucellus.

The exceptions to the preceding case may be explained as follows: While incipient embryo development frequently precedes pollination, in some instances this development does not begin until after the stigma is receptive to pollen. If, in the latter case, a pollen tube reaches the embryo sac before parthenogenetic development begins, it will not be impossible for the diploid egg to be fertilized. (It is also conceivable that a haploid egg from a functioning macrospore can be fertilized on some occasions.) Since, moreover, the chromosome behaviour is frequently irregular in the meiotic divisions of the microsporocytes, the male gamete which fuses with the egg may not possess a true haploid number, and consequently a zygote formed from such a union will possess an aneuploid number of chromosomes. Once the hybrid is produced, the newly combined chromosome complements, either euploid or aneuploid, will be transmitted to future generations by parthenogenesis.

It seems possible to conclude that the singular characteristics of *P. pratensis*, namely, polymorphism and varying aneuploid chromosome numbers as

between biotypes, and constant morphological type and chromosome number in plants of the same biotype, can be explained on the basis of the known parthenogenetic development of diploid eggs in embryo sacs arising from nucellear cells, and by the possibility of an occasional fertilization of an egg by a male gamete possessing possibly a deviated chromosome number.

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TISCHLER, G. ***Die Bedeutung chromosomaler Rassedifferenzen für Systematik und Pflanzengeographie***

In den letzten Jahren ist es möglich geworden, bei einer grossen Zahl von Arten polyploide Rassen zu erhalten. Die Methoden sind mannigfacher Art. Ich nenne hier nur die vermittelst Colchicin oder Acenaphten. In der Natur haben sich in erster Linie, wahrscheinlich hervorgerufen durch Temperaturschocks oder wechselnde Hydratur, bei einem Teil der Arten die Auto- oder Allopolyploiden restlos durchgesetzt, bei anderen kennen wir diploide und polyploide Rassen nebeneinander, endlich sind viele Arten rein diploid geblieben.

Augenblicklich (Juli 1939) gelten die nachstehenden Zahlen für die Angiospermen folgender Länder:

Land	Artenzahl	Chromosomal untersucht (%)	Diploid (%)	Polyploid (%)	Diploide u. Polyploide möglich (%)
Schleswig-Holstein	1074	927 = 86·3	437 = 47·1	430 = *46·4*	60 = 6·5
Norrland (Schweden)	973	754 = 77·5	322 = 42·7	380 = *50·4*	52 = 6·9
Faröer	266	220 = 82·7	83 = 37·7	125 = *56·8*	12 = 5·5
Island	358	268 = 75·4	88 = 32·8	164 = *61·2*	16 = 6

Diese Übersicht zeigt uns deutlich, besonders wenn wir Flovik's Erfahrungen über *ca.* 80 % Polyploide in der Flora Spitzbergens dazunehmen, dass, je weiter wir in Europa nach Norden kommen, destomehr die Zahl der Polyploiden zunimmt. Dazu passt der Befund an der Angiospermen-Flora Schleswig-Holsteins. Von den Pflanzen, die ihre Hauptverbreitung im Süden haben, sind z.Zt. 90·4 % bekannt; davon sind nur 32·9 % Polyploide und 4·3 % unsicherer Stellung, während die mit einer Hauptverbreitung nach Norden zu 81·6 % bekannt sind, 66·9 % Polyploide und 9·4 % "Unsichere" enthalten.

Arwidsson's Skepsis bezüglich der Übertragung von Chromosomenbestimmungen auf beliebige Individuen verschiedener Zonen ist demnach vorläufig nur für wenige Prozente berechtigt. Zum gleichen Resultat kam jüngst Turesson.

Aber gerade diese *ca.* 6 % obiger Angiospermen-Floren, die wir auf *ca.* 16 % erhöhen könnten, wenn wir nicht nur die chromosomal verschiedenen Rassen des betreffenden Landes, sondern der ganzen Erde berücksichtigen, sind für die Cyto-Ökologie und Systematik besonders dankbare Objekte. Im ganzen kennen wir bereits über 400 "Coenospecies" mit chromosomendifferenten Rassen, und natürlich wird diese Zahl noch gewaltig zunehmen.

In einer Reihe von Fällen ist, worauf zuerst Hagerup hinwies, mit der Polyploidie eine grössere Widerstandsfähigkeit einer Art gegenüber dem Gesamtklima des Nordens oder alpiner Höhen direkt nachgewiesen. Hierher gehören z.B. *Nasturtium officinale* und *Biscutella laevigata* (Manton), *Empetrum nigrum* (Hagerup), *Opuntia polyacantha* (Stockwell), *Vicia cracca* (Sweschnikowa, Senn), *Pentstemon azureus* (J. Clausen) *Veronica prostrata* (Scheerer), *Tradescantia canaliculata* (Anderson u. Diehl), *Tripsacum dactyloides* (Mangelsdorf u. Reeves), *Phleum alpinum* und andere Gräser (Müntzing), *Dupontia Fisheri* (Flovik). Dabei ist nicht ohne weiteres anzunehmen, dass die Resistenz gegen die tiefsten Temperaturen die entscheidende Rolle spielt. Diese kann offenbar stark wechseln, hat doch z.B. im Experiment Schlösser festgestellt, dass autotetraploide Rassen von *Solanum lycopersicum* gegenüber ihren diploiden Eltern einen geringeren osmotischen Druck und verringerte Widerstandsfähigkeit gegen Kälte besitzen, während für die gleiche Art Kostoff das Umgekehrte angibt.

Viele Charakterpflanzen des Nordens oder der Berge sind gerade ausgesprochene Diploide, z.B. *Draba nivalis* und *fladnizensis*, *Arabis alpina*, *Ranunculus glacialis* und *pygmaeus*, *Thalictrum alpinum*, *Dryas octopetala*, *Sibbaldia procumbens*, *Diapensia lapponica*, *Phyllodoce coerula*, *Cornus suecita*, *Veronica alpina* und *fruticans*. Die Parallele zu den halophilen Gewächsen, die Wulff und ich in Schleswig-Holstein, Tarnavschi in Rumänien, untersuchten, springt in die Augen. Bei *Vaccinium uliginosum* (Hagerup), *Artemisia borealis* (Erlandsson), *Ranunculus auricomus* und *Campanula rotundifolia* (Böcher), für die di- und tetraploide Rassen bekannt sind, haben sogar nur die Tetraploiden die Konkurrenz mit den anderen Gewächsen im "klimatisch günstigeren" Süden aufnehmen können. Und *Arenaria serpyllifolia* (Griesinger) wie *Fritillaria camtschatcensis* (Matsuura) und *Narcissus bulbocodium* (Fernandes) konnten sich im diploiden Zustand allein in

Bergeshöhen halten, während sie sich im Tiefland zwar viel weiter verbreiteten, aber nur als Polyploide.

Gerade unsere Unkräuter zeigen sehr oft klar die Bedeutung der Polyploidie für die Gesamtverbreitung. Von vielen kennen wir auch ihre diploiden Rassen (häufig unter einem "besonderen" Speciesnamen), diese haben aber im Gegensatz zur Hauptrasse nur geringe lokale Verbreitung erlangt. So verhalten sich z.B. *Capsella bursa pastoris* (Shull), *Fumaria officinalis* (Wulff, Negodi, Sugiura), *Stellaria media* (Peterson, Negodi), *Polygonum aviculare* (Jaretzky), *Erodium cicutarium* (Warburg, Gauger), *Solanum nigrum* (Winkler, Bhaduri), *Poa annua* (Avdulov, Stählin, de Litardière, etc.). Aber auch "Nichtunkräuter" verdanken ihre Hauptverbreitung der Polyploidisierung, wie die gleichfalls noch vorhandenen diploiden Rassen beweisen, so *Spiraea chamaedryfolia* (K. Sax), *Pimpinella saxifraga* (Håkansson), *Iris aphylla* und *Triticum* (*Agropyrum*) *elongatum* (Simonet), *Deschampsia flexuosa* (Hagerup), *Orchis maculatus* (Hagerup, Vermeulen, Heusser). Einen recht charakteristischen Wechsel ihres Standortes haben dabei *Dactylis glomerata* (Müntzing) und *Myosotis silvatica* (Geitler) vorgenommen. Als Diploide kennen wir sie aus Wäldern, als Polyploide von Fettwiesen. Eines der schönsten Beispiele bietet aber wohl *Salicornia herbacea*. Hier haben sich bisher alle Rassen des mediterranen Gebietes und des centraleuropäischen Binnenlandes als diploid gezeigt (Tarnavschi, König); auf dem Schlickwatt der Nordsee sowie auf Flugsand vermögen allein die Tetraploiden oder Hypertetraploiden zu gedeihen (Wulff, König); ja es wurde experimentell nachgewiesen, dass auf diesen Böden die Diploiden bald absterben. Für *Honckenya peploides* (Rohweder) oder *Triticum* (*Agropyrum*) *junceum* (Simonet) liesse sich sogar an eine selektive Wirkung innerhalb der verschiedenen bisher nachgewiesenen Grade der Polyploidie auf Salzboden denken. *Honckenya* ist bisher von schwach salzigen Böden der Ostsee mit $n=24$ Chr., von stärker salzigen der Nordsee mit $n=32$ Chr. bekannt, während *Triticum* an Nordsee und Atlanticküste nur Individuen mit $n=14$, im Mittelmeer mit $n=21$ zu besitzen scheint.

Selbstverständlich ist die Polyploidie stets nur innerhalb bestimmter Grenzen möglich. Der weitverbreitete Glaube, dass eine ökologische Schwächung sich auch in einer Herabsetzung der Organgrösse zu erkennen geben muss, ist aber nicht allgemein richtig. Ich arbeite z.Z. an der Zytologie einer Rasse von *Phragmites communis* mit Riesenwuchs, die gegenüber der normalen tetra- oder hypertetraploid ist (vielleicht auch octoploid, da die Normalrasse selbst schon tetraploid sein dürfte). Diese Rasse hat aber—zum mindesten nicht in Europa—die gewöhnliche nicht zu verdrängen vermocht. Riesenwuchs braucht also nicht immer das für die Verbreitung einer Art "günstigste" Merkmal zu sein. *Aloe ciliaris* (Resende) ist z.B. gewöhnlich hexaploid; allein eine pentaploide Rasse zeigt Riesencharaktere. Und jetzt auf den Congress lernen wir als schönes Beispiel *Osmunda regalis* (Manton) kennen. *Rumex acetosa* (Yamamoto) kann hexaploid kleine Organe als triploid haben, und *Paspalum Urvillei* (Nielsen) ist mit $2n=20$ chrom. kräftig als mit 30.

Innerhalb der Gesamtart ist die Polyploidisierung sicherlich öfters vor sich gegangen und kann verschiedene diploide Rassen getroffen haben. Shull's ausgedehnte Studien an *Capsella bursa pastoris*, oder Miss Manton's an *Biscutella laevigata* reden da eine sehr eindringliche Sprache. Hier liegt eine Fülle von Themen zur Bearbeitung offen. *Rumex acetosa* und Verwandte, *Anemone nemorosa*, *Valeriana officinalis*, die heimischen Mentha-Arten, *Heleocharis paluster* und viele andere "Coenospecies", die Müntzing zusammenstellte, versprechen mit Sicherheit interessante Resultate.

Mit Allopolyploidie kann eine besondere Arealausdehnung verbunden sein. Müntzing's synthetisch hergestellter *Galeopsis*-Bastard, *Galium verum* × *mollugo* (Homeyer, Fagerlind), *Spartina stricta* × *alterniflora* (Huskins) und vor allem Babcock und Stebbin's *Crepis*-Hybriden sind allbekannte Beispiele dafür. Auch Flovik's "kryptopolyploide" *Festuca*-Rassen gehören wohl hierher. Hier konnte allein aus den Chromosomenformen die Einkreuzung von *Festuca rubra* in Rassen von *Festuca ovina* sichergestellt werden.

Oft, aber durchaus nicht immer, scheint bei annuellen Arten mit der durch die Polyploidie verlangsamten Entwicklung Perennieren ausgelöst zu werden (Müntzing). Man denke dabei auch an solche Artenpaare wie *Scleranthus annuus* und *perennis*, *Obione pedunculata* und *portulacoides*, *Helianthus annuus* und *tuberosus*, *Urtica urens* und *dioica*, *Anthoxanthum aristatum* und *odoratum*. Hohe Wahrscheinlichkeit besteht schon jetzt, dass der jeweils an zweiter Stelle genannte Partner einmal durch Amphidiploidie entstand. Und nicht nur Hinausschieben der Bildung der Sexualorgane, sondern auch deren Ersatz durch irgend eine Form von Apomixis, sofern eine ererbte Neigung dazu bereits bei den Diploiden bestand, kann durch Polyploidie gefördert werden. *Ficaria verna* (Negodi, Larter), *Allium roseum* (Messeri); *Festuca*- und *Poa*-Arten (Turesson, Müntzing, Flovik, u.a.), *Agaven* (Vignoli u.a.) können sich polyploid oft nur durch Bulbillen oder Brutzwiebeln vermehren. Ja bei *Festuca ovina* fand Turesson sogar, dass die Apomikten des schwedischen Festlandes mit $2n=21$ Chr. einen niedrigeren Grad von Polyploidie

als die der Lofoten und Faröer mit $2n=28$ besassen. Nur eine Rasse des Jemtlandes (mit $2n=42$) machte eine Ausnahme. Die oben bereits genannte *Fritillaria camtschatkensis* (Matsuura), *Hemerocallis fulva* (Belling), wahrscheinlich auch *Acorus calamus* (Wulff) haben ihre grosse Verbreitung nur als sterile Triploide erlangt. Für die Fälle somatischer Parthenogenesis liegt die Beziehung zwischen Geschlechtsverlust und Polyploidie klar zu tage. *Taraxacum-*, *Hieracium-*, *Chondrilla-*, *Antennaria-*, *Alchimilla-*, *Potentilla-*, *Rosa-* und wohl auch *Sorbus-* und *Rubus-*Arten u.a. liefern viele Beispiele.

Ganz kurz sei nur an Fagerlind's Funde bei "saisondimorphen" verschiedenchromosomigen *Galium*-Arten erinnert, deren Sommerrassen diploid, deren Herbstrassen polyploid sein können. Wie sich R. v. Wettstein's saisondimorphe Gentianen und Euphrasien verhalten, wissen wir noch nicht. Einige Funde von v. Witsch bei letzteren geben Hinweise, dass auch hier Ähnliches vorkommen könnte.

Über das ökologische Verhalten von $(n+1)$-Rassen in freier Natur wissen wir noch fast gar nichts. Wir kennen sie fast ausschliesslich von künstlich erzeugten sog. "doppelt Trisomen" bei *Datura*, *Oenothera* und anderen Arten. Freilich sind zahlreiche Fälle mit überzähligen Chromosomen, sogar bei Kulturpflanzen (*Secale*, *Linum*, etc.) bekannt. Aber man streitet noch über die Entstehung des neuen idiogramms. Die Chromosomen könnten durch Disjunktion oder Fragmentation vorhandener zustande kommen. Im letzteren Falle wäre ein Erhaltenbleiben anscheinend nur möglich, wenn gerade die Centromere quer durchschnitten werden, sodass jedes der neuen Chromosomen einen Teil davon bekäme. Neuere Funde von Mrs Darlington (Upcott), u.a. zeigen, dass das in der Tat möglich ist. Kommt dann noch bei Kreuzungen die Bindung beider mit je einem Chromosom einer verwandten Rasse dazu, so wäre die Beweiskette geschlossen. Genaue Kenntnis der Idiogramme einer Art ist die Voraussetzung für solche Schlussfolgerungen. Wulff fand für *Jasione montana*, dass bisher alle untersuchten Individuen aus einer Dünenrasse der Nordsee $n=7$ Chr. aufwiesen, während der Art sonst allgemein nur $n=6$ Chr. zukommen. $(n-1)$-Rassen werden meistens bei Diploiden nicht lebensfähig sein. Einfache Fusionen zweier Chromosomen zu einem werden wegen der doppelten Centromere bei der nächsten Meiose Störungen hervorrufen. Wir wissen z.B. nicht, wie die 6-chromosomigen Rassen von *Vicia cracca* entstanden sind, die Frl. Sveshnikova in engster Umgebung von Moskau auffand, während im übrigen die Art 7- resp. 14-chromosomige Rassen besitzt. Ökologisch wissen wir von solchen Rassen nichts.

Turesson würde alle bisher behandelten verschiedenchromosomigen "Rassen" als "Teilarten" seiner "Coenospecies", als "Ökospecies", werten können. Sehr zahlreiche Arten gehören sicherlich noch hierher, von denen wir z.Zt. eine Verbindung mit der Ökologie noch nicht kennen, z.B. die von Winge, u.a. studierten Rassen von *Erophila verna* oder die von *Poa pratensis* und anderen Gräsern, die namentlich schwedische Autoren untersuchten. Mahnend muss uns Müntzing's Ausspruch vor Augen stehen: "Not a single case is known, in which it has been demonstrated that intraspecific chromosome races are ecologically identical." Morphologische Differenzen brauchen nicht auffällig hervorzutreten. Klassisch dafür ist Miss Blackburn's *Silene ciliata* geworden. Aber auch *Knautia arvensis*, *Agrostemma githago*, *Lotus corniculatus*, u.a. wären hier vielleicht zu nennen.

Wenden wir uns nun zu den Arten mit "oscillierenden" Zahlen, die ihren Ursprung wohl einem Bastardisierungsprozess, ähnlich dem bei *Viola tricolor* × *arvensis* (J. Clausen), verdanken. *Viola canina* und *V. Battandieri*, *Saxifraga granulata*, *Prunus laurocerasus*, *Iris pseudacorus*, *Poa alpina*, *Arum maculatum*, vielleicht auch *Sedum telephium*, *Crepis biennis*, *Cr. ciliata* und neuerdings *Cr. modocensis* sind bekannte Beispiele. Von letzterer sagen Babcock und Stebbins, dass fast jede Chromosomenzahl zwischen $2n=33$ bis 88 gefunden werden könne. Es dünkt mir sinnlos, wollten wir hier für jede chromosomal verschiedene Sorte von Individuen einen eigenen Rassen- oder Ökospecies namen geben. Untersuchungen über sonstige zelluläre Unterschiede, wie z.B. bez. der Zellgrösse fehlen noch völlig. Sollte sich Gleichheit zwischen chromosomal verschiedenen Individuen finden, könnte man auch an sekundär erworbene Gleichheit im Sinne F. v. Wettstein's denken, der allmähliche Herabregulierungen der Zellgrössen bei bivalenten Rassen von *Bryum caespiticium* feststellte. Die ursprünglichen *Gigas*-Charaktere konnten dabei verloren gehen, während die Fertilität sogar noch stieg.

Leider wissen wir auch fast gar nichts über die Ökologie der Rassen, die sich nur durch veränderte Chromosomenformen auszeichnen. Am besten bekannt ist hier *Matricaria inodora*, deren Acker-, Sand- und Felsenrassen Chromosomen von verschiedenem Volumgehalt aufweisen (Hüser). Nielsen fand jüngst zwei Rassen mit scharf unterschiedenen Chromosomenformen bei *Andropogon scoparius*. Wie weit die mit verschiedenen Satelliten ausgezeichneten Rassen von *Iris spuria*, die neulich Westergaard auffand, verbreitet sind, wäre noch festzustellen. Vorläufig zeigen die österreichischen und dänischen Individuen die genannten chromosomalen Verschiedenheiten. Tarnavschi fand gleichfalls vor kurzem, dass die am Schwarzen Meer wachsenden Individuen von *Kochia*

hirsuta schlankere Chromosomen zu besitzen scheinen als die an der Nordsee. Wenn *Zostera nana* so viel voluminösere Chromosomen besitzt als *Z. marina* (Blackburn, Wulff), so zeigt dies, dass auch mit erhöhter Chromatinzunahme eine Verkleinerung der Organe verbunden sein kann. Bei eingehenderen Studien müssten überall genauere Abgrenzungen gegenüber modifikativen Wirkungen der Umwelt vorgenommen werden. An erheblichen genotypischen Unterschieden ist aber schon jetzt nicht zu zweifeln. Die von mir so genannten "Pseudogigas-Rassen", die wir z.Zt. für *Phragmites*, *Primula*, *Narcissus*, *Trifolium*, *Petunia*, u.a. Arten kennen, sind m.W. auf ihre ökologische Bedeutung überhaupt noch nicht untersucht. Die Möglichkeit, die grösserchromosomigen Rassen unter Umständen im Sinn von Negodi als "kryptopolyploide" zu deuten, ist wohl noch gar nicht erörtert. Hier darf auch Rohweder's Fund einer Mutante von *Dianthus plumarius* erwähnt werden, die an Stelle der charakteristischen 45 kleinen 15 grosse Chromosomen besass.

Schliesslich sind die durch Chromosomen-"Umbau", d.h. durch Translokationen, Inversionen, Deletionen oder ähnliche Vorgänge veränderten Chromosomenrassen zu erwähnen. Sie bedingen, sofern die Veränderungen in grösserem Ausmass vorkommen, weitgehende Sterilität bei der Kreuzung mit den ursprünglichen Rassen und die Möglichkeit geographischer Isolierung. Blakeslee und Mitarbeiter haben das in grossem Umfang für *Datura stramonium* festgestellt. Von sonstigen Erfahrungen sei hier nur auf Geitler's schöne Studien an *Paris quadrifolia* verwiesen, der innerhalb einer Population das gleichzeitige Vorhandensein vieler derartiger chromosomal verschiedener Rassen auffand. Charakteristisch war dabei Möglichkeit vegetativer Vermehrung.

Russische Forscher (M. Nawaschin, Schkwarnikow, Kostott) haben gezeigt, dass in der Natur wie im Laboratorium solcher Chromosomenumbau durch Temperatureinflüsse verbunden mit abnormer Feuchtigkeit und Überaltern der Samen zustande kommt, und im Prinzip gleiches wie bei Behandlung mit kurzwelligen Strahlen erreicht wird. Müntzing's schönes Sammelreferat auf dem letzten deutschen Genetikertag hat das alles so eingehend behandelt, dass weitere Ausführungen sich hier erübrigen.

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Tomasson, H. ***Investigations on Heredity of Manic-depressive Psychosis in Iceland***

While working for 9 years as a specialist in Iceland, 1928–36, the author has diagnosed 859 more or less severe cases of manic-depressive psychosis. 129, i.e. 15·2%, of these were treated in a hospital.

It can be maintained with a fairly high degree of probability that the diagnosed cases represent the majority of cases of this disease which have occurred in Iceland during the time of observation.

The frequency of this form of disease in the country could therefore be calculated at an annual percentage of 0·14 during the time of observation. There is hardly any statistically important difference in the frequencies in men and women.

In 653 cases, the patient's age at the first onset of the disease is recorded. It would seem as if the disease mostly manifests itself between the ages of 20 and 42 years, with the maximum frequency around 33 years, but a closer investigation seems to show that if we are to speak of a "danger zone" it lies between 15 and 69 years.

The total probability for the disease that an individual of 15 will develop a manic-depressive affection before the age of 70 is 0·07. 50% of the risk of falling ill with this disease is passed in women at the age of 35, in men at the age of 40, 80% when a woman reaches the age of 50, 75% when a man reaches the age of 50.

A group of twenty-five manic patients were more closely examined. Data were collected on all individuals born in their families, the descendants of the grandparents, making up a corrected number of 2463 individuals at the ages of 15–70 years in the period of observation.

The frequency of disease in this group selected at random corresponds to the one applying to the population at large, both from a general neuropsychiatric and a special manic-depressive point of view, and accordingly it constitutes a certain guarantee that the examiner has actually observed the majority of the cases which occurred during the period of observation.

Consanguinity is only present once among the parents. Manic-depressive psychosis is found once among the parents. Among the sibs of the primary cases, manic-depressive psychosis occurs ten times, or in 7·1% of the cases.

Rüdin found approximately the same percentage among the sibs of manic-depressive patients whose parents were healthy. Strömgren also found about the same figure for the sibs of the patients who had close on 9% of manic-depressive parents. The present author finds the same values for the probable frequency of manic-depressive "genes" in the population at large.

It would consequently seem as if nothing definite can be stated at present regarding the hereditary mechanism for the manic-depressive psychosis, or indeed whether it may be considered to be hereditary so far as this material is concerned.

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TSCHERMAK VON SEYSENEGG, E. ***Weitere Beobachtungen über hybridogene Pseudoparthenogenesis***

Schon seit mehreren Jahren konnte ich an Leguminosen, aber auch an Cruciferen wie *Cheiranthus*, *Matthiola* und *Erysimum* im Anschlusse an fremdartige Bestäubung mehrfach Fruchtansatz beobachten nach frühzeitigem Entfernen der eigenen Staubbeutel und Schutz vor sonstiger Bestäubung. Allerdings blieb die Frucht- und Samenentwicklung wie bei den genannten Cruciferen auf einer gewissen jugendlichen Stufe stehen, oder es fiel wie bei den Leguminosen der bereits als "gelungen" betrachtete Fruchtansatz zur Enttäuschung des Experimentators wieder ab. Und doch handelte es sich nicht, wenigstens nicht durchwegs um Fruchthüllenentwicklung ohne Befruchtung, wie solche Fälle von Parthenokarpie an samenlosen Weinrassen seinerzeit durch Müller-Thurgau festgestellt wurden. Vielmehr kam in meinen Versuchsreihen doch hie und da ein Same zur Ausbildung und Reifung und lieferte nicht etwa einen intermediär-konstanten Bastard, wie ich solche zwischen verschiedenen Gattungen von Gramineen, speziell zwischen *Triticum* und *Aegilops* oder *Haynaldia* als *Aegilotricum* und *Haynaldtricum* erzeugen konnte (ab 1926).[1] Im Gegenteil resultierten in den hier behandelten Fällen elter- und zwar muttergleiche Individuen, die sich weiterhin als ebenso fruchtbar und konstant erwiesen wie reine Vertreter der Mutterart. Da in Kontrollversuchen an denselben Arten ohne jede Bestäubung kein Fruchtensatz erfolgte, also spontane Entwicklung ohne Befruchtung ausgeschlossen war, durfte ich von Fällen hybridogener Parthenogenesis oder Pseudogamie sprechen und die Vorstellung vertreten, dass der fremdartige Pollen eine Entwicklungserregung der Samenknospe verursacht habe, ohne selbst etwas an Ermasse beizutragen. Allerdings möchte ich gleich auch hier die Annahme wiederholen, dass die fremdartige Pollenzelle zwar primär Befruchtung, das heisst Zutritt ihres Zytoplasmas wie ihres Kerns zur Eizelle bewirkt, ihre Erb- beziehungswiese Kernmasse in dem fremdartigen Milieu jedoch sekundär ausgeschaltet wird, wie dies Jörgensen (1928), an seinen Präparaten der Kreuzung *Solanum nigrum* × *S. luteum* nachweisen konnte. Ich spreche daher von einer hybridogenen Pseudoparthenogenesis und betrachte ein solches Verhalten als Grenzfall von wirksamer Verbindung zweier Formen. Nach meiner Auffassung führt eben eine Stufenleiter sexueller Affinität vom reinen freien Mendeln, wie wir es zwischen nahverwandten Rassen beobachten, über das korrelativ beschränkte oder gebundene Mendeln, weiterhin über die intermediär-konstante Vererbungsweise, die ich auf Chromosomenaddition ohne Geminibildung und Genenaustausch beziehe, schliesslich zu dem hier behandelten Grenzfall hybridogener Pseudoparthenogenesis oder Pseudogamie. Was die Kernkonstitution ihrer Produkte anbelangt, so wäre zunächst an den gesamten somatischen Zellen wie an den Gameten der pseudoparthenogenetischen Individuen reine Haploidie zu erwarten. Erst von der nächsten Generation ab würde der normale Wechsel in der Garniturenzahl eintreten. Doch sei es als nicht ausgeschlossen bezeichnet, dass schon an den Produkten hybridogener Pseudoparthenogenesis Haploidie durch einmaliges Unterbleiben von Zellteilung nach Kernteilung zur normalen vollwertigen Diploidie aufreguliert werden könnte. Solch ein Regulation könnte sich eventuell auf bestimmte Teile des Pflanzenkörpers beschränken (vgl. Beobachtungen von J. Loeb (1921) an Echinodermenkeimen. Ob, wann und inwieweit eine solche Möglichkeit in meinen Beobachtungsfällen verwirklicht ist, oder ob der einfachste Fall einer haploiden Erstgeneration zutrifft, möchte ich vorläufig ganz dahingestellt sein lassen. Bezügliche Untersuchungen sind erst im Gang. Auch ist bei Pflanzen, welche mit echtem Endosperm, also mit doppelter Befruchtung im Sinne von Nawaschin und Guignard ausgestattet sind, mit der Möglichkeit eines verschiedenen Verhaltens von Eizelle und Embryosack zu rechnen. Fremdartiger Pollen könnte hier einerseits zu einer typischen, nachhaltigen Befruchtungswirkung am Endosperm führen, und zwar unter glatter Addition der fremdartigen Chromosomensätze. Andererseits könnte der zweite Kern desselben Pollenkornes zwar in die Eizelle eindringen und dieselbe—unter Zytoplasmogamie—zur Entwicklung anregen, selbst aber zu Grunde gehen. Es würde also ein pseudoparthenogenetischer völlig muttergleicher und ursprünglich haploider Embryo nebst einem additiv bastardierten Endosperm resultieren, wobei letzteres bei Dominanz der patroklinen Färbung sogenannte Xenien in der ersten Samengeneration (jedoch ohne Erbwert für spätere Generationen!) zeigen könnte. Dieser interessante Mischfall mag verwirklicht sein bei meiner Kreuzung von blaukörnigem Weizen × gelbkörnigem *Lolium*, wobei Xenienbildung nämlich gelbe Korn- bezw. Endospermfarbe (welche hier gegenüber blau dominiert) auftrat. Ob hier der Embryo selbst pseudoparthenogenetischen, also primär haploiden Charaktern trug, muss allerdings erst die zytologische Analyse lehren. Natürlich ist auch der umgekehrte Fall (additiver Embryo mit pseudoparthenogenetischem Endosperm) denkbar. Besonders aber ist

[1] Dass sich diese Abstufung nicht notwendig gleichmässig auf alle unterscheidenden Merkmale, also auf den Gesamthabitus der beiden gekreuzten Formen bezieht, sondern dass die einzelnen Erbeinheiten sich verschieden (freimendelnd, korrelativ-gebunden, intermediär-additiv) verhalten können, braucht hier nicht näher ausgeführt zu werden.

damit zu rechnen, dass in dem einen Falle, beziehungsweise an den einen Samen eine wahre Bastardnatur des Embryos wie des Endosperms in dem anderen Falle bezw. an den anderen Samen hingegen Pseudoparthenogenesis des Embryos und wahre Bastardierung des Endosperms oder auch Pseudoparthenogenesis beider Anteile des Samens vorliegt. So wären gerade manche Fälle von Mischsamigkeit nach fremdartiger Kreuzung verständlich! Es bestehen eben bei der Doppelbefruchtung bezw. Entwicklung von echtem Endosperm vier Möglichkeiten von wirksamer Befruchtung oder von hybridogener Parthenogenesis jedes Samenanteiles. Natürlich wird man sich schwer entschliessen, ein so mühsames und selten erzieltes Produkt dem Zytologen glatt zu opfern und nur ein vorsichtiges Abschneiden einzelner Wurzelspitzen an den vorgekeimten, sodann ängstlich angebauten Samen gestatten.

Doch bin ich gleich mit theoretischen Erklärungen vorausgeeilt und möchte nur noch kurz eine Übersicht meiner neuen Beobachtungsdaten geben. Die erste Mitteilung (Seysenegg, 1935) hatte Kreuzungsfälle von Leguminosen betroffen und zwar *Pisum arvense* oder *sativum* × *Vicia sativa* und reziprok, ferner *Pisum arvense* × *Vicia Ervilia*, sodann Erbse × Linse sowie Wicke × Linse, Erve × Linse und reziprok, endlich Erve × *Vicia sativa*. Heute kann ich über folgende Ergänzungen berichten, welche analoge Fälle nach künstlicher Kreuzung zwischen verschiedenen Arten, ja Gattungen von Getreide betreffen.

Zunächst waren es Winterweizen und Wintergersten, welche nach sorgfältiger Kastration mit Pollen von Gräseren bestäubt und zuverlässig gegen sonstige Bestäubung geschützt in nicht wenigen Fällen reife Samenkörner erbrachten, die zum Teil bereits weiter angebaut wurden und F_1 Pflanzen entstehen liessen. Schon wenige Tage nach der Bestäubung trat ein Anschwellen zahlreicher Samenknospen ein, die aber frühzeitig oder erst später eintrockneten, während sich aber doch in einzelnen Fällen Aehren ab und zu ein und das andere Korn ganz oder ziemlich normal entwickelte.

So erhielt ich im Jahre 1938 von Winterweizen × *Lolium italicum* in drei Ähren 4+1+3, also acht Körner, welche 1939 angebaut, reinen, muttergleichen Winterweizen produzierten. In diesem Jahre ergaben solche Kreuzungen in fünf kastrierten Ähren sechs ausgereifte Körner.

Von der im Jahre 1938 ausgeführten Kreuzung Winterweizen × *Festuca pratensis* wurden in vier kastrierten Ähren 3+2+2+2, also neun Körner gewonnen, die 1939 muttergleiche Produkte ergaben.

Ein fruchtbares *Aegilotricum* gab 1939 mit *Lolium italicum* gekreuzt in einer kastrierten Ähre ein schwachentwickeltes Korn.

Zweizeilige Sommergersten gaben 1938 mit *Hordeum bulbosum* gekreuzt in zwei kastrierten Ähren 3+3, also sechs Korn, welche 1939 reine muttergleiche Individuen erzeugten.

1939 wurden aus der Kreuzung zweizeilige Wintergerste × *Hordeum murinum* in Zwei kastrierten Ähren 3+1, also vier Körner gewonnen.

Zweizeilige Wintergersten wurden 1938 und 1939 mit Winterroggen gekreuzt.

Ergebnis: aus drei kastrierten Ähren: 3+2+1, also sechs Körner. Die im Jahre 1939 angebauten zwei Körner ergaben wieder muttergleiche Pflanzen.

Zweizeilige Wintergersten wurden 1938 und 1939 mit Winterweizen gekreuzt.

Ergebnis: aus acht Ähren, die Ansatz zeigten 3+2+1+1+2+2+2+1, also vierzehn Körner. Die 1938 gewonnenen Körner ergaben 1939 gebaut wieder völlig muttergleiche Individuen.

Winterweizen mit Gerste gekreuzt gab im Jahre 1939 nur in einer kastrierten Ähre ein gut entwickeltes Korn.

Schliesslich erzielte ich 1939 aus einer Bestäubung sorgfältig kastrierter Blütchen einer Ähre eines Sommerweizens mit Pollen von *Lilium candidum* drei gut entwickelte Körner.

Auch scheinen Fälle hybridogener Parthenogenesis bei gewissen Primulaceen vorzukommen.

Wahrscheinlich besteht auch die Möglichkeit, dass bei den Versuchen seltene Art- oder Gattungsbastarde zu erzeugen wie z.B. bei Bestäubungen zwischen Weizen und Roggen oder Weizen × *Aegilops* und anderen Gräsern (oder bei solchen reziproken Bestäubungen) in einzelnen Fällen Samen entstehen, aus denen wirklich gelungene Bastarde, eventuell auch unfruchtbare oder fruchtbare Additionsbastarde erwachsen können, oder aber, dass aus den durch die Bestäubung gewonnenen Samen wieder muttergleiche Individuen entstehen, die ihre Abkunft einer hybridogenen Parthenogenesis verdanken. Das Entstehen gut entwickelter, keimfähiger Samen bei selten gelingenden Art- und Gattungbastardierungen, die in ihren Nachkommen wieder den rein mütterlichen Typus reproduzieren, muss demnach nicht unbedingt immer auf ungewollte Selbstbestäubung infolge mangelhafter Kastration, wie man bisher annahm, zurückgeführt werden. Vielmehr ist bei Samenansatz nach Fremdbestäubung unter allen gebotenen Vorsichtsmassnahmen und Hervorgehens völlig elter- bezw. muttergleicher Tochterindividuen mit der Möglichkeit hybridogener Parthenogenesis oder Pseudogamie bezw. Plasmogamie zu rechnen.

Zum Schlusse möchte ich nur bemerken, dass die Zahl meiner älteren wie neueren Beobachtungsfälle zusammen doch schon eine ganz stattliche zu nennen ist, und dass ich bei der Sorgfalt, die ich auf Grund dezennienalter Erfahrung auf Kastration, Bestäubung und Schutzmassregeln verwendet habe, durch-

aus nicht an eine Täuschung glauben kann. Gewiss entbehren meine züchterischen Beobachtungen noch der vollen Sicherung durch den Nachweis einer wenigstens temporären Haploidie an den als hybridogen parthenogenetisch betrachteten Produkten.

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TURPIN, R., PITON, J. *et* CARATZALI, A. *Recherche sur les corrélations leucocytaires des jumeaux*

L'examen des jumeaux peut contribuer à la solution des problèmes héréditaires quand les résultats qu'il fournit sont comparés à ceux d'enquêtes complémentaires. Avec cette pensée, nous avons entrepris l'étude des leucocytes sanguins de jumeaux mono- et dizygotes. Nos premiers résultats ont trait à la formule d'Arneth.

Le matériel utilisé, 96 individus, se décompose ainsi qu'il suit:

Monozygotes: 14 paires (8 ♀ et 6 ♂).
Dizygotes de sexe identique: 12 paires (7 ♀ et 5 ♂).
Dizygotes de sexe différent: 7 paires.

En outre 30 sujets, dont 19 ♀ et 11 ♂, ont été examinés et 11 d'entre eux, 7 ♂ et 4 ♀, l'ont été deux fois pour servir de base de comparaison pour l'étude de la corrélation intra-individuelle.

Corrélation entre formules d'Arneth. Le coefficient de corrélation a été calculé en prenant la moyenne des lobes nucléaires des granulocytes neutrophiles.

L'intervalle de variation aléatoire du coefficient de corrélation chez les monozygotes va de +0·6877 à +0·9624.

La corrélation est donc très fortement positive. En comparaison, l'étude de la corrélation intra-individuelle nous a montré que la différence entre z (Fisher, 1938) intra-individuel et z des monozygotes n'est pas significative. Par conséquent, il est probable que le phénomène se présente d'une façon identique dans les deux cas.

Chez les dizygotes de sexe identique, l'intervalle de variation aléatoire du coefficient de corrélation va de −0·5025 à +0·5929 et chez les dizygotes de sexe différent de −0·7997 à +0·5425. Ces résultats ne sont pas significatifs.

Les résultats mentionnés indiquent, par conséquent, la possibilité d'une détermination héréditaire de la formule d'Arneth.

Corrélation entre formule d'Arneth et taux des granulocytes neutrophiles (calculés en pourcentage du total des granulocytes). La corrélation entre ces deux phénomènes (r. = −0·1288) ne semble pas assez grande pour qu'on lui rattache une signification.

Formule d'Arneth et sexe. La différence des moyennes obtenues entre les sexes est significative. Dans nos échantillons, la déviation vers la gauche de la formule d'Arneth est plus fréquente chez la femme que chez l'homme sans que nous sachions si ce fait dépend de facteurs génétiques.

Formule d'Arneth et âge. L'analyse de la fluctuation (variance) a été effectuée séparément chez les ♂ et chez les ♀, pour écarter l'erreur qui pourrait tenir à l'inégale répartition, entre les différents échantillons envisagés, des deux sexes, dont la constitution est dissemblable. Cette analyse nous montre que la formule d'Arneth ne paraît pas influencée par l'âge, tout au moins après la première année, car nos sujets les plus jeunes sont âgés de un an.

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TURRILL, W.B. *Taxonomy and Cytogenetics in Plants*

The limitations of taxonomy and of taxonomists are so well known that the basic importance of systematics is sometimes overlooked. It is difficult to imagine that biology could have started in any other way than by a recognition of similarities and dissimilarities between individuals and the grouping together of individuals with common characters. It is also easy to understand how attributes useful to man were correlated with gross morphological characters, and for a long period were together the only ones available for classification. It is desirable for several reasons that the taxonomist should be, in practice, relatively conservative, and it is only within recent times that the taxonomist concerned with the seed-bearing plants has realized that the data made available by his colleagues since the advent of the compound microscope, the refinement of experimental technique, and the application of chemico-physical methods to biological problems are often able to help in establishing a more widely useful classification.

The incorporation of anatomical and even of biochemical data in the orthodox scheme of botanical classification presents little difficulty. Cytogenetic data are different in that they offer the chance of developing a more dynamic system of classification but may upset a static one considerably. For example,

if cytogenetics cannot provide increasingly valuable sign-posts to phylogeny taxonomists will be justifiably disappointed. While the cytogeneticist has his own peculiar realm of research and his own special problems, there is, intermediate between taxonomy and genetics, a wide field of research which has been very little investigated. Some of the problems with which the taxonomist most wants help are not such as appeal to the cytogeneticist, either because of intrinsic difficulties connected with the material—such as the large numbers of small and poorly fixing chromosomes in *Saxifraga*—or because the problems do not seem to be sufficiently exciting. On the other hand, some cytogeneticists who have done extremely specialized research seem now to be taking a wider view of biological problems, and there are welcome signs of a new linkage between even such extremes as genes and geography. The object of this paper is to suggest problems, to the cytogeneticist, within the limits of the Spermatophyta, which, though essentially taxonomic, require his kind attention. Some of the problems to be mentioned have already received notice from cytogeneticists, but in a limited or casual manner. The plea is made, or more accurately is supported, for it has been made before, that deliberate, long-range, co-operation between taxonomists and cytogeneticists is overdue. The practical means by which individuals and institutions can be linked up for this purpose are under investigation by the Association for the Study of Systematics in Relation to General Biology.

The arrangement of the suggestions here made is one of convenience under a number of headings, and the sequence of these does not indicate their relative importance.

I. Classifications of characters

The material at the disposal of the taxonomist consists of phenotypes, often of dead samples representing phenotypes. Long before the dawn of modern genetics, however, the taxonomist had recognized the distinction between phenotype and genotype and, in theory, maintained that his species, at least, were distinct genotypes or groups of genotypes. What, with partial exceptions, he failed to put into practice was simple experimental testing. The need for a full study of plasticity is becoming more and more obvious in modern taxonomy. How widely can the characters controlled, within limits, by genes be expressed in morphological and physiological variants? Under what range of phenotypes could any one genom carry an organism through one complete or partial life history? The Transplant Experiments of the British Ecological Society at Potterne have thrown some light upon this problem for a limited number of species and for a very limited range of environmental conditions. Some genotypes (as those included in *Plantago maritima*) are highly plastic, even to the extent that characters considered by a recent author as subspecific and varietal have been induced in one and the same genotype by soil differences alone. Others are (when grown on different soils) extremely stable, but may or may not show different death rates. Till such experimental data are available genotypes cannot be classified as phenotypically plastic or stable, nor can two phenotypes be classed with certainty as modifications of one genotype. Different species and even different genotypes within the species behave so differently that controlled experiments alone can determine the nature and degree of plasticity. The following genera would well repay detailed study of plasticity, even restricting research to a few of their species and to British material: *Ranunculus*, section *Batrachium*, *Polygonum*, *Stellaria*, *Helianthemum*, *Polygala*, *Arenaria*, *Sagina*, *Hypericum*, *Erodium*, *Sedum*, *Callitriche*, *Daucus*, *Asperula*, *Scilla*, *Mentha*, *Thymus*, *Chenopodium*, and *Atriplex*.

The degree and kind of morphological and physiological plasticity has important ecological and evolutionary bearings. The more plastic a genotype the greater is the number of communities in which it is likely to occur and the greater will be its chance of survival.

The taxonomist evaluates the characters he uses. Some he considers to have specific, others generic, and others family value. This evaluation has been almost entirely based on the coherence of attributes, so far as the system made is a "natural" one. Characters which, when used in classification, group together plants (or groups of plants) having most attributes in common are selected as having diagnostic value at every taxonomic grade. Can cytogenetics give any independent criterion of taxonomic value of characters? Have characters designated specific by the taxonomist any cytological basis or genetic behaviour different, as a class, from the basis or behaviour of characters used as varietal or generic? Is the taxonomist cytogenetically justified in splitting *Pyrus* s.l. into *Malus*, *Sorbus* and *Pyrus* s.s., of separating *Celsia* and *Verbascum* on the basis of stamen number, making numerous species of *Viola* (section *Melanium*), *Taraxacum*, *Centaurea*, *Erodium*, *Orchis*, and *Salicornia* within the limits of the British flora?

Closely connected with the evaluation of characters is the question of the number and uniformity of taxonomic grades. Are the usually accepted grades sufficient or are more wanted? Are "species" all of the same value or does the category "species" require splitting into several to many different grades? The cytogeneticist can surely give many new facts helping towards the solution of such problems.

II. Degree of correlation of characters

The so-called "natural" classification of seed plants has been made mainly by using the principle of the maximum correlation of characters, combined with selection and "weighing" of characters. Yet "exceptions" are frequent when any character which is accepted as usually diagnostic for a group is traced throughout the members of the group. What is the cytogenetical mechanism which controls, for any group, the usually high correlation of characters, many of which are apparently trivial from an adaptational or survival standpoint, but permits of occasional failure in the coherence of the same characters? For example: Have the pseudo-monocotyledons peculiar cytogenetic structure or behaviour? Are herbaceous members of mainly woody families and arborescent members of mainly herbaceous families cytogenetically peculiar? What gene control is there of the inferior ovary in *Samolus* as compared with that for the superior ovary of the vast majority of the Primulaceae? What cytogenetically makes parasitism obligatory in *Cuscuta* while holophytism is shown by other genera of the Convolvulaceae? How is the habit explained cytogenetically for the very few aquatic members of the great family Compositae? Can cytogenetics suggest how gamopetaly is nearly always associated with syncarpy, yet exceptions occur as in Crassulaceae? There are hundreds of such "breakdowns" in complete correlation known to taxonomists, and their cytogenetic investigation might well throw light upon the phylogeny of particular groups and on general evolutionary problems.

III. Constitution of taxonomic groups

Taxonomists, in the Spermatophyta, limit their diagnoses almost entirely to morphological criteria. The number of species and genera which have been studied cytogenetically is now sufficiently great for a serious consideration of the possibilities of a general use of cytogenetic data additional to others. Such correlations of taxonomic (i.e. essentially morphological) and cytogenetic data as have been made have usually appeared in connexion with cytogenetic and not taxonomic research. There are still so many cytogenetic uncertainties and so many gaps in the data that the conservatism of the taxonomists has some justification. On the whole, it appears that cytogenetics gives strong support to much taxonomic work, though relatively small improvements in classification are frequently suggested.

The taxonomic treatment of polyploids, in such a genus as *Tulipa*, is a problem urgently needing the combined attention of taxonomists and cytogeneticists.

The publication of the Merton Catalogue, under the auspices of the Association for the Study of Systematics in Relation to General Biology (*New Phytologist*, Reprint No. 20, 1939) is welcomed by taxonomists and must give a stimulus to co-operation between taxonomists and cytologists.

IV. The study of polymorphic groups

The adjective polymorphic is here used in the taxonomic sense to qualify species, genera, etc., which are accepted to include individuals of widely diverse characters relative to the grade, or whose characters show low correlation. The treatment of highly polymorphic groups has not been uniform. This is partly because the polymorphism is due to different causes in different groups. High plasticity, high gene-mutation rates, the occurrence of mutations having no or a low selective value, chromosome changes and irregularities, hybridization, and wide geographical range are, singly or in combination, some of the causes. Probably most species are much less uniform than is realized, because the taxonomist usually has limited material for study and from that selects his diagnostic characters, largely ignoring those he considers of little or no classificatory value. The cytogeneticist is already giving help to the taxonomist in such polymorphic genera as *Rubus*, *Rosa*, and *Viola*. A cytogenetic study of *Verbascum* and *Celsia* would have recent taxonomic monographs as a basis. The batrachian *Ranunculi*, if studied from a combined taxonomic, cytogenetic, and ecological standpoint, would provide exciting material, once initial technical difficulties of cultivation were overcome. The genus *Thymus* is easy to grow from seed, has many species hardy in this country, and its taxonomic difficulties should interest the cytogeneticist. The firs (*Abies*) of the Nearer East and the lilies (*Lilium*) of the Balkan Peninsula have also unsolved problems of polymorphism.

V. Geographical and ecological problems

The taxonomic value of data of an ecological and phytogeographical nature has long been recognized. The work of Prof. Tischler and others shows that cytogenetics can throw light on certain problems of geographical distribution. An extension of cytogenetic research to groups showing marked kinds or peculiarities of ecological or phytogeographical distribution is suggested. Ecological paramorphs of an ecotype nature, such as *Cytisus scoparius* var. *prostratus*, *Solanum dulcamara* var. *marinum*, and *Centaurea nemoralis* var. *minima* are under investigation. Paramorphs with more or less clearly delimited geographical distribution include *Gentiana lutea* subsp. *symphyandra*, *Glaucium luteum* var. *leiocarpum*, and *Ranunculus Ficaria grandiflora*. Relict genera and species, such as those of the European Gesneriaceae,

need their cytology compared with that of their geographically distant taxonomic allies. Species, genera, or families with discontinuous distribution (often but not always of a relict nature) need comparative cytological investigation and, when possible, genetical experiment, as in *Dianthus caesius*, *Arbutus*, *Empetrum*, and Monimiaceae. The cytogenetics of feral species or those recently established through human agency might give valuable information on problems of isolation, since cytogenetic changes could be approximately dated. The synthetic study of genera with wide or peculiar geographical range, such as *Erica*, should yield data of importance to the taxonomist and phylogenist. The introduction by Dr Huxley of the useful word cline, suggests that suitable clines should be cytogenetically investigated. Such a study of the *Fagus sylvatica-orientalis* group, which partly forms a complicated cline, would assist the taxonomist in clearing up some of his problems regarding the beeches in Europe and western Asia.

VI. Hybridization in nature and in experiment

The commoner occurrence in plants than in animals of fertile natural hybrids and of hybrids between taxonomically less closely related individuals is an important difference between the plant and animal kingdoms. In addition to mating preferences, mobility, the absence of a gametophyte generation (and especially of its complete retention within spores) found in animals, there may well be also some general cytogenetical "causes" involved at one stage or at more than one. Hybridization is certainly common in plants when congeners meet and ecological selection (in the broad sense) and geographical isolation appear to be relatively more important than in animals as causes of speciation. The branching habit with often numerous apical meristems, combined with the rarity of definite sex chromosomes, and the prevalence of hermaphroditism, allows fertile allopolyploids, such as *Spartina Townsendii*, to be made naturally, perhaps on a far wider scale than is yet known. Wide crosses (such as between individuals belonging to two subfamilies in Cyperaceae) would mean that allopolyploidy by somatic chromosome doubling could establish a new and distinctive group with wide possibilities for further differentiation, through mutation, secondary polyploidy, secondary hybridization, etc.

The evolutionary importance of hybridization is increased by the occurrence of "bridging" groups, as in *Anagallis*, a phenomenon recalling that known for certain kinds of parasitism. Plants A and C may be infertile with one another, but each is fertile with B. An indirect gene exchange, if nothing more, is then possible between A and C.

In connexion with hybrids, not necessarily species hybrids, a comparison by deliberate experiments of the degree of plasticity of homozygotes (for certain investigated factors) and of the corresponding heterozygotes may be urged. There is some evidence that heterozygotes are sometimes more, sometimes less, plastic than their homozygous parents.

VII. Problems of apomixis

The taxonomist wishes to determine the extent of apomixis and to deal in the most practical way with apomicts. In some groups, as in the British Taraxaca so far tested, apomixis seems constant, and a large number of morphologically more or less clearly differentiated apomicts occur. In some plants, possibly in many, apomixis is of casual occurrence—frequent, for example, in *Ranunculus Ficaria* but relatively rare in *R. acris*. Taxonomic treatment of apomicts has not been uniform. Some taxonomists ignore them, others make them varieties, subspecies, or species. In Druce's *List of British Plants* nearly 100 apomicts of *Taraxacum* are listed as species and more have been described since. Babcock and Stebbins in their fine work on American species of *Crepis* describe apomicts as subordinates to species. By not giving Latin descriptions they avoid the names given to apomicts being subjected to the International Rules of Nomenclature. This is not very important, for the Rules may be altered to validate descriptions in English and made retrospective, and even as they stand the Rules allow for additional taxonomic grades being made if required. There is no doubt that the occurrence and behaviour of apomicts complicates the species concept. As a working hypothesis in *Taraxacum* I consider it advisable, for the present, to consider apomicts as neither species nor paramorphs of species but simply as a category of their own. The dogmatic statement in the International Rules of Nomenclature that every plant belongs to a species, unless it be a hybrid or a chimaera (the word hybrid being defined as a hybrid between two species), should be repealed as a possible hindrance to taxonomic progress.

VIII. Problems of phylogeny

Taxonomists can themselves be classified. One possible grouping is into those who make practical classification itself the only or final aim and those who try to find causal explanations of deeper biological problems in the results or extension of taxonomic research. The former are not infrequently, within a limited sense, the better taxonomists. The activities of the latter are usually directed into one or both of two extra spheres of investigation. Either phylogeny or environment and geographical distribution, or both, strongly engage their attention. Unfortunately in the Angiosperms available palaeonto-

logical data are of very little use in tracing phylogeny, apart from the difficulties of incorporating such data in classification. Consequently phylogenetic schemes have to be based on other and often less satisfactory data. The result has been the publication of very different hypotheses. There is, therefore, an important possibility of cytogenetic data giving assistance in judging the value of rival theories. There are plenty to choose from. A phylogenetic system for Angiosperms involves a consideration of the origin of the group. Is it monophyletic or polyphyletic? Recent researches have undermined the basis of some of the strongest arguments for a monophyletic origin—thus we now know that there is great and fundamental important diversity in the development of the megaspore and gametophyte, in the structure of the carpel, and in the nature of the perianth. How far such diversities can be correlated with important differences in cytology and genetic behaviour may perhaps be determined by a comparison of data already available. How far cytology and genetics can throw light on phylogeny of larger groups is still an open question, but the fundamental basis of heredity and evolution is certainly the cytogenetic system, and this may be expected to retain signs of its previous history and we have to learn to read them aright.

The following is a brief discussion of a few of the problems on which the phylogenist especially needs new data. What are the relationships of taxonomically isolated groups or of groups of uncertain affinities? The Adoxaceae, Plantaginaceae and Callitrichaceae are well-known examples. Are "simple" structures reduced or primitive? How can convergence and parallelism be distinguished from evolutionary continuity? What is the genetical significance of the reticulation of characters which is so prominent a feature of classifications based on morphological characters? What is the cytogenetic explanation of the fact that some taxonomic groups show "tendencies" or "progressions" in certain characters that are fixed in other groups? Is the taxonomist cytogenetically justified in giving a different value to the same or similar characters in different groups? Are certain genes in some sense more deeply seated or so placed as to mutate less readily than others? Is there any means of determining by cytogenetic research the absolute or relative age of such character combinations as appear to be fairly permanent and which are used for the diagnosis of taxonomic groups? Is a given character, for example, gamosepaly or gamopetaly, due to one or to how many genes or gene combinations? The incorporation of the increasing number of available cytogenetic facts into phylogenetic theorizing may well lead not only to a solution of these and similar questions but also to a reconsideration from a sounder basis than is yet possible of the wider problem as to how far a phylogenetic system of classification is possible for the Angiosperms.

IX. General suggestions

The following suggestions are given somewhat categorically and without the support of facts and details which they deserve. They are, to the taxonomist, self-evident truisms which, however, are not always recognized, or at least put into practice, by the cytogeneticist. Samples of all material used in cytological and genetic research should be accurately determined and preserved by herbarium or museum methods for future reference. There are well-known researches whose published results the taxonomist hesitates to use, not because the cytology or genetics is wrong, but because he is uncertain that the determination of the material was correct and he has no means of checking it owing to the absence of preserved samples. The taxonomist also realizes more often than the cytogeneticist the need for examination of material from as many different stocks as possible before wide generalizations can safely be drawn. Differences in counts or behaviour of chromosomes in what is supposed to be one and the same species may be due to wrong determination or to cytological diversity within the species. It would be unbecoming for a taxonomist to suggest mistakes in the cytological research itself.

The taxonomist would welcome more and more cytogenetic investigation of wild material of ecologically and geographically localized origin. This is not to minimize the importance of research on cultivated plants and domesticated animals, but there are general problems of biology that can only be solved when facts obtained by experiments with organisms long and specially selected by man are tested for organisms direct from the wild and by the study of naturally occurring populations. The taxonomist can often aid the cytogeneticist by obtaining for him authentically named and fully localized wild material. Of particular botanical interest would be the cytogenetic investigation of tropical plants on a scale that must wait the establishment of numerous suitably equipped research stations in the tropics.

It may be hoped that in this brief and all too dogmatic statement of some of the problems of mutual interest to the taxonomist and the cytogeneticist the latter will find some satisfaction in the indications that his important researches are being appreciated and used by an ever widening circle of taxonomists who desire closer and closer co-operation. In our own section of this Congress—Genetics in relation to evolution and taxonomy—members will expect to find general questions discussed and synthetic approaches to the great problems of biology advocated. We trust they will not be disappointed.

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VANDEL, A. ***The Genetics of Sexuality in Terrestrial Isopods.***

Terrestrial Isopods have conspicuous peculiarities in sex ratio. Many species show an example of distribution of sexes called *monogeny*, which is rare in the animal kingdom. Some of the females, called *monogenic*, give offspring which are all, or largely, of one sex; other females, called *amphogenic*, give offspring comprising both sexes.

I have previously studied (Vandel, 1936–9) monogeny in three species belonging to three very different families: *Trichoniscus provisorius* (family Trichoniscidae), *Chaetophiloscia elongata* (family Oniscidae) and *Armadillidium vulgare* (family Armadillidiidae). Monogeny has also been reported in *Armadillidium vulgare* by H. W. Howard (1938).

The proportion of both female types, monogenic and amphogenic, differs according to the species, and within a species, according to locality. I bred 392 females of *Trichoniscus provisorius*, collected in the country; the study of their offspring showed that 304 were amphogenic and eighty-eight monogenic, consequently 22·4 % of monogenic females. In *Armadillidium vulgare*, among fifteen females, seven were amphogenic and eight monogenic. Monogeny is then frequent in this species.

Monogenic and amphogenic females are, morphologically and physiologically, similar. Offspring of monogenic females, apart from the distribution of the sexes, are entirely normal.

Monogenic females are divided into *arrhenogenic* and *thelygenic*, the first producing males, the second producing females. Monogenic females---either arrhenogenic or thelygenic—are either *perfect*, if their offspring include, besides a majority of specimens of one sex, a few of the other sex. I observed, in *Trichoniscus*, *allelogenic* females, producing successive broods, some of which show arrhenogenic characteristics, others thelygenic characteristics.

In *Trichoniscus provisorius*, among the monogenic females, the number of arrhenogenic females exceeds that of thelygenic females (181 arrhenogenic and seventy-seven thelygenic observed in my cultures). Among *Armadillidium vulgare*, arrhenogenic females are as frequent as thelygenic (the eight monogenic females observed include four arrhenogenic and four thelygenic). Therefore, in *Armadillidium vulgare*, the sex ratio of the offspring of monogenic females seems, on the whole, quite normal; the eight monogenic females produced 730 males and 691 females. Consequently, statistics built upon collections cannot reveal monogeny in this species; but breeding experiments alone are able to show the anomalies of sex ratio.

On the other hand, in *Chaetophiloscia elongata*, statistics at once show a strong disturbance in sex ratio. Arcangeli (1931) observed, in Italy, a proportion of males of 13·6%. Verhoeff (1931) collected, in Italy, eight males and fifty-nine females, males 12%. Strouhal (1936) counted, in a collection from Corfu, seven males and ninety-two females, males 7%. I collected, at Toulouse, 522 specimens: sixty-eight males and 454 females, males 13%.

Contrary to the affirmation of Arcangeli (1925), I showed that parthenogenesis is not present in this species. Females, isolated since their birth, remain sterile; when these females are mated, they breed normally. The disturbance of sex ratio, in this species, is the result, not of parthenogenesis, but of monogeny. In this species, the females are, in major part, thelygenic, and therefore, the sex ratio is strongly disturbed.

Similar conditions occur in another species, *Chaetophiloscia sicula*. The sex ratio is very abnormal in this form: Verhoeff (1931) collected, in Italy, eighteen males and seventy-two females, i.e. 20% of males. Among 157 specimens collected at Toulouse, I counted thirteen males and 144 females, i.e. 8·2% of males.

The males exert no action on monogeny. Males from arrhenogenic females have been mated with amphogenic females. The offspring of these pairs never showed the characters of monogeny. Therefore, the arrhenogenic females do not transmit their properties to their sons.

Monogeny depends only on the female. This peculiarity is inheritable and follows the rule of maternal inheritance. The monogenic females transmit their properties to their daughters which are themselves monogenic. I studied carefully, in *Trichoniscus provisorius*, this type of inheritance which is less regular than mendelian inheritance. The sexual type may pass from one generation to another without modification, or may reverse entirely (for instance, the daughters of a thelygenic female are all arrhenogenic), or may reverse partially (for instance, some of the daughters of a thelygenic female are arrhenogenic, others thelygenic).

Monogeny is probably connected, in terrestrial Isopods, with female heterogamety. This fact is as yet uncertain, because sex-linked mutations are not certainly known in terrestrial Isopods (see, however, Vandel, 1939 *d*).

Assuming that, in terrestrial Isopods, the female is heterogametic, one may suppose that, in monogenic females, the orientation of the heterochromosomes on the maturation spindle is constant and determines the formation of ova all corresponding to the same sexual type. This study may throw light upon the almost unknown question of the orientation of chromosomes on the spindle.

I studied, in *Armadillidium vulgare*, a colour mutation which seems very similar to the variety *cooperi* of

Collinge (1917). This mutation is determined by a single, dominant gene. I studied the offspring of three monogenic females, heterozygotic for the gene *cooperi*. The offspring of these females, mated with normal males, showed typical segregation; both parental types were equally represented. Disjunction of autosomal genes is then normal, in the monogenic females, while distribution of sex genes follows a preferential system.

Both types, arrhenogenic and thelygenic, are determined by the constant orientation of the heterochromosomes; this orientation depends upon the cytoplasmic constitution of the ova. The constitution of egg cytoplasm does not result exclusively from genic action; this condition can be modified by external and ontogenic agents, operating during development. Therefore the constitution of the egg-cytoplasm, and, in consequence, the distribution of the heterochromosomes and of the sexes, can be modified experimentally. I showed that, in *Trichoniscus*, temperature can modify sex-ratio in the offspring of imperfect monogenic females. The effect of raising the temperature to 20–22° C. is to diminish the proportion of females and to increase the proportion of males. This case is very similar to that of the Psychid, *Talaeporia tubulosa*, studied by J. Seiler (1920). Distribution of the heterochromosomes results from the constitution of the egg cytoplasm which depends upon non-genic agents such as temperature and over-ripening.

In these cases then we can modify experimentally the sex ratio.

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VANDENDRIES, R. et GAVAUDAN, P. ***Remarques concernant l'action de la colchicine et de l'acénaphtène sur quelques organismes inférieurs***

Nous avons précédemment abordé l'étude de l'action de la colchicine sur les euglènes, les levures, les basidiomycètes et les bactéries (Vandendries et Gavaudan, 1939). Tous ces organismes nous ont paru réfractaires à l'action de la colchicine. D'autres essais nous ont montré que divers *Polytoma*, divers infusoires, les *Gonium*, les *Closterium* et les *Micraster* étaient insensibles à l'action de la colchicine.

Depuis le début de l'année 1938 nous avons fait de nombreux essais à la colchicine sur les basidiomycètes. Ces champignons possèdent une remarquable immunité à l'action de la colchicine et peuvent développer leurs carpophores, apparemment normaux, sur milieux fortement colchicinés. Nous avons suivi la germination des spores de *Coprinus radians* en milieu liquide colchiciné à 1 par 100. Le développement de l'utricule et du tube germinatifs est entièrement normal. La même concentration est également bien tolérée par *Euglena gracilis* et permet la multiplication de cet organisme. La cause de l'immunité de nombreux êtres inférieurs à l'action de la colchicine n'est pas élucidée et nous avons déjà indiqué (*loc. cit.*) quelques hypothèses possibles à ce sujet. D'autre part dans une note préliminaire où nous annoncions une étude de l'action des hydrocarbures, nous avons avancé que ces substances n'étaient que difficilement transformées par les organismes inférieurs. A la réflexion il semble qu'il ne faille pas sous-estimer la possibilité d'une transformation des hydrocarbures par la cellule (on sait que les carbures cancérigènes, par exemple, subissent des transformations dans l'organisme). *A priori* il n'est donc pas prouvé qu'en faisant agir sur les organismes inférieurs des substances stathmocinétiques à constitution hydrocarbure on élimine la possibilité d'une immunité résultant d'une action métabolique.

Quoi qu'il en soit, nous avons étudié l'influence de l'acénaphtène sur la germination des spores de *Coprinus radians*. Dans une goutte de liquide nutritif maintenue en huile de paraffine, sur lame creuse, il faut introduire un grand nombre de cristaux d'hydrocarbure pour provoquer par rapport aux témoins un retard de germination, avec épaississement et arrêt de croissance du tube germinatif. L'action est plus intense et les résultats sont plus homogènes en faisant agir en chambre humide les vapeurs d'acénaphtène sur les spores plongées dans une goutte pendante. La saturation en hydrocarbure du milieu et des spores paraît s'effectuer plus rapidement partir des vapeurs qu'à partir des cristaux. On obtient également un retard de germination et un gonflement anormal du tube germinatif par exposition des spores sèches pendant 3 à 24 heures aux vapeurs d'acénaphtène, avant la mise en chambre humide. L'étude cytologique n'a pas encore été faite, mais il semble bien qu'il ne s'agit que d'un arrêt banal de la croissance.

Nous avons aussi essayé l'action de l'acénaphtène sur *Euglena gracilis*. Les cristaux mélangés aux cultures finissent par tomber au fond des ballons de

culture. Les cultures sont agitées doucement de temps en temps. Dans ces conditions l'acénaphtène ralentit la multiplication des euglènes et exerce même une action toxique, si la quantité de cristaux est trop grande. Les cultures traitées sont beaucoup moins vertes que les cultures témoins, puis jaunissent, mais les euglènes ne présentent pas de modifications permettant de supposer qu'il y a eu stathmocinèse. L'acénaphtène semble donc sans action sur certaines cellules, bien qu'étant nettement stathmocinétique sur les végétaux supérieurs. D'autre part, comme il manifeste une certaine toxicité (ralentissement de croissance ou de multiplication), il pénètre donc dans les cellules traitées, sans que celles-ci soient sujettes à des altérations caryocinétiques. Il faut rapprocher cette absence d'action spécifique de l'acénaphtène sur certains organismes inférieurs, des résultats négatifs obtenus sur les cultures de fibroblastes d'embryon de poulet.* Des essais sur la souris effectués avec Mr N. Kobozieff nous ont montré que l'animal de 20 grammes supportait sans dommage l'injection de plusieurs centigrammes (0·03 g.) d'acénaphtène en solution huileuse.

Ces résultats préliminaires sur l'action de la colchicine et de l'acénaphtène sur les organismes inférieurs indiquent: (1) que les deux substances, bien que douées d'une puissante activité stathmocinétique sur les phanérogames, en paraissent dépourvues sur divers organismes inférieurs; (2) que l'acénaphtène possède une certaine toxicité pour quelques organismes inférieurs; (3) que l'inactivité de l'acénaphtène sur certains organismes inférieurs est à rapprocher de celle constatée, au moins dans certaines conditions, sur la cellule des animaux supérieurs.

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VERSCHUER, O. VON. ***Bemerkungen zur Gen-Analyse beim Menschen***

Unter Genanalyse versteht man gewöhnlich die Analyse der Erbanlagen in den Chromosomen einer Spezies. Der höchste Grad dieser Forschung ist bei *Drosophila* und einigen anderen Tier- und Pflanzenarten erreicht, von welchen heute Genkarten vorliegen. Dasselbe Ziel strebt auch die Erbforschung beim Menschen an. Allerdings sind hier die Forschungsmöglichkeiten eng begrenzt und zwar aus zwei Gründen: (1) An die Stelle des Experiments muss eine mühsame Materialsammlung treten; (2) der Mensch besitzt neben dem Geschlechtschromosom 23 Autosomenpaare. Die Wahrscheinlichkeit der Koppelung zweier Erbanlagen ist deshalb nicht sehr gross.

Beim Menschen wurde die Genanalyse normaler Eigenschaften versucht. Der Erbgang dieser Merkmale ist aber meist ein recht komplizierter. Eine Sonderstellung nehmen die Blutgruppen ein, von welchen wir die *A–B–R*-Reihe multipel-alleler Gene und die allelen *M–N*-Gene als die hauptsächlichsten Vertreter kennen; sie sind in zwei verschiedenen Autosomen lokalisiert.

Die erbpathologische Forschung hat sich in der vergangenen Zeit mit besonderer Energie der Erforschung der Erblichkeit der Nerven- und Geisteskrankheiten zugewandt. Die Ergebnisse sind für die eugenische Praxis von grösster Bedeutung, für die Genetik dagegen noch wenig befriedigend—sind wir uns doch noch nicht einmal einig über den Erbgang der hauptsächlichen Vertreter dieser Krankheitsgruppe, wie Schwachsinn, Schizophrenie, Manisch-depressives Irresein und Epilepsie!

Am fortgeschrittensten ist die Genanalyse von den krankhaften Eigenschaften des Auges und von den körperlichen Missbildungen. Zahlreiche Erbmerkmale sind in ihrem Phänotypus und auch nach ihrem Erbgang genau bekannt. Die körperlichen Anomalien, die durch eine Entwicklungsstörung im Knorpel-Knochensystem zustande kommen, sind ausschliesslich durch autosomale, meist dominante, seltener rezessive Gene bedingt. Unter den krankhaften Erbanlagen des Auges finden sich dagegen neben einer Mehrzahl von autosomalen dominanten und rezessiven Anlagen auch im Geschlechtschromosom gelagerte Erbanlagen. v. Verschuer und Rath haben Faktorenaustausch zwischen den beiden *X*-Chromosomen einer Frau, und zwar für die Bluter—und die Rotgrünblindheitsanlage, nachgewiesen. Haldane hat den ersten Versuch der Aufstellung einer Genkarte des *X*-Chromosoms des Menschen unternommen. Weitere Fortschritte auf diesem Wege sind zu erwarten. Auch wird es mit der Zeit gelingen, unter den autosomalen Genen bestimmte Koppelungsgruppen herauszuschälen.

Für die weitere Forschung sind methodische Erfahrungen der letzten Zeit wichtig: Umfassende Zwillingsforschungen sind notwendig, um für alle häufigeren Erbmerkmale diejenigen phänogenetischen Fragen zu untersuchen, die sich allein mittels der Zwillingsmethode klären lassen. Die statistische Auswertung von Familienmaterial zur genetischen Analyse setzt die Kenntnis der Beziehung zwischen Gen und Ausseneigenschaft voraus. Die Vernach-

* Nous prions M. le Dr J. Verne, Professeur à la faculté de Médicine de Paris et M. le Dr J. André Thomas, chef de laboratoire à l'institut du Radium, qui ont bien voulu, indépendamment, réaliser ces essais et nous autoriser à en faire état, d'accepter nos bien vifs remerciements.

lässigung dieser grundlegenden Forderung hatte in der vergangenen Zeit zu unnützem Streit um Erbhypothesen bei einzelnen Krankheiten geführt. Weiterhin ist es wichtig, dass die Erbanalyse nicht nur an einigen wenigen besonders "interessant" erscheinenden Familien, sondern an unausgelesenen Serien von Familien, ja an ganzen Bevölkerungsgruppen durchgeführt werden. Derartige grossangelegte systematische Zwillings- und Familienforschungen und erbbiologische Bestandsaufnahmen sind in Deutschland unter Einsatz mehrerer Forschungsinstitute im Gange. Sie finden eine wesentliche Unterstützung durch die staatliche Gesundheitspflege, die mehr und mehr zu einer Krankheitskartei der ganzen Bevölkerung ausgebaut wird. Aus dieser planvollen Arbeit ergeben sich ganz besonders günstige Möglichkeiten der weiteren Erbanalyse beim Menschen.

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VOGT, O. ***Variation as seen in the Light of Topistic Diseases of the Brain***

The central nervous system contains many different kinds of nerve cells characterized by size and shape of the cellular body, its inner structure and that of the dendrites, by the number and site of origin of the dendrites, and by their neurites which differ in length, diameter, thickness of the sheath and way of ending. The cell bodies of each kind of nerve cells are found in a particular part of the brain. If such a district contains other nerve cells, these cells frequently also exhibit a peculiar structure. Often the same holds for the glia. The blood vessels also may show specificity in number and arrangement, and from their isolated disease in such a district the conclusion of a special structure of their walls seems justified. Such districts acquire the character of *organs* by the harmonious development of their tissue elements. The sharp demarcation of neighbouring districts should be emphasized in that connexion.

We call such districts *topistic regions* or *grisea*. Each tissue element which characterizes such a *griseum* represents an *elementary topistic unit*.

Illustration of the foregoing facts on the corpus striatum and the globus pallidus and on the striate area.

We call all primary diseases of a griseum or of a single of their topistic units a *topistic* or *systematic disease*.

Such topistic diseases, when investigated in detail, demonstrate:

(1) by their being exactly restricted to topistic units that the structure of the tissue determines the site of the disease;

(2) a "pathoclisis" common to man (or other species) in general, i.e. a tendency of certain structural elements to be injured by certain damaging agents;

(3) the causation of unusual individual or family predispositions (pathoclises) by the unusual structure of the diseased topistic units;

(4) the different character of the lesions if the whole brain is involved;

(5) usually the disease of *several* structural units which are not closely linked by connecting fibres;

(6) frequently a definite order in which the disease spreads;

(7) often a parallelism between the severity of the disease and its time of onset (both being signs of its "expressivity");

(8) features typical for the particular etiology;

(9) that diseases are not extremely uncommon which are probably new mutations.

Illustration on diseases of the corpus striatum and those grisea which are connected to it and of the cortex cerebri.

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WAARDENBURG, P.J. (1) ***Concerning Dominant X-chromosomal Inherited Eye Defects in Man.*** **(2)** ***Concerning Recessive and Intermediary X-chromosomal Inheritance in Man***

(1) No completely typical dominant sex-linked character has yet been encountered, but in addition to an "irregularly" dominant skin disease there are a number of eye diseases showing the same mode of inheritance. In other pedigrees these conditions behave as recessives, and the question therefore arises as to whether we are dealing with one and the same gene in different environments (genome, constitution, etc.) or with different genes. *Dystrophia retinae pigmentosa* and *extraocular nystagmus*, for example, can behave as dominant or recessive autosomals as well as dominant or recessive genosomals. In certain pedigrees of haemophilia and of disturbances of colour vision, for example, the carrier shows partial expression of the character. Are we dealing with the results of crossing-over? There are probably two or more loci concerned in disturbances of colour vision. The genes behave as multiple allelomorphs, and the lesser disturbance is dominant over the more serious. Other characters possibly have the same kind of genetic basis. It must not be forgotten that commonly irregularity in a pedigree is merely an indication of that pedigree's imperfection and incompleteness. Often the number of normal males and females do not agree with the theoretical expectation, there being an excess of affected males and heterozygous females in respect of sex-linked characters.

(2) There are many instances in which a character disobeys the rules of recessive sex-linked inheritance. In the case of abnormalities of colour vision it is suggested that there are two independent series of multiple allelomorphs, a proto-series mainly concerned with disturbances of redivision and of green vision, and a deutero-series concerned with the opposite effects. In both series normality is dominant over feeble perception and this over colour blindness. A phenotypically normal female can carry in each *X*-chromosome a gene of a different series. There are pedigrees in which the same defect of colour vision is exhibited by about half the males, whilst, exceptionally, full brothers can belong to different types. In two pedigrees linkage between vision disturbance and haemophilia has been demonstrated. There were two kinds of males, those with and those without the two characters. In other pedigrees half the sons are haemophilics and half have colour disturbances, the mother having carried a gene for a different defect in each of her *X*-chromosomes. In another pedigree there is evidence that a phenotypically normal mother (with a haemophilic brother) possessed an *X* with the genes for haemophilia and deuteranomalia, and that her husband showed deuteranopia.

There is some evidence of intermediary inheritance. In the case of haemophilia many carriers show slight retardation of coagulation. In colour blindness it is established that in the proto-series about 40% of carriers can show symptoms of abnormal colour vision. Intermediary inheritance probably occurs also in choroideremia; in a skin disease with secondary inflammation of the cornea through distichiasis; in retinitis pigmentosa with myopia; in atypical pigmentation of the retinae and choroid; in congenital cataract; and in certain defects of the teeth and hair, e.g., Thadani's family with absence of teeth, and that of Huskins with absence of the central incisors.

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WADDINGTON, C.H. ***The Mechanism of the Genetic Control of Development***

Most recent advances in our knowledge of genic action have come from studies of the effects of genes on fairly simple developmental processes. It often seems, in fact, that our knowledge advances the more rapidly the simpler the process which is under investigation, and that our aim should be to find some example in which the action of the genes can be immediately stated in chemical terms. This is indeed an important objective, and investigations such as those of Beadle and Ephrussi on *Drosophila* eye pigments, and Scott Moncrieff, Price and others on flower pigments, in which this goal has been to some extent attained, are without question among the most valuable advances which have recently been made.

But an analysis in chemical terms of the simplest developmental processes will not in itself be sufficient to obliterate the disturbing hiatus which separates the genetical and the embryological chapters in our theories of development. Embryogenesis involves the appearance of highly complex entities—organs and tissues. However profoundly we may believe that the processes concerned must eventually be stated only in chemical terms, the fact remains that a chemical analysis of histogenesis and organogenesis lies in the future. We can only regard such phenomena as involving systems of chemical processes, each of which may be analogous to the production of a single substance such as a pigment. In order to obtain a point of view on the problem of how genes control development, we require not only to have some idea as to how genes are related to the unit processes of chemical change, but also as to their relations to the more complicated systems of processes which cause the formation of organs and tissues.

The mechanisms of development are considerably different in different groups of animals, and it is still not entirely clear whether they can all be considered as variations on a single fundamental type. But if any one type can be taken as basic, that can only be the organizer reaction of Spemann. We have here a developmental process which gives rise to a product, the neural plate, which is complex enough to be taken as representative of the entities which are formed during embryogenesis. And, further, this is almost the only case in which the developmental process can be seen to involve a reaction. It depends on an inductive stimulus coming from the mesoderm and affecting the overlying ectoderm. In many other phenomena of development, the mechanism is, as it were, less spread out to view; the process takes place, and development occurs, within a single mass of tissue, as it would if we imagined the organizer intimately mingled with the reacting tissue. We can therefore probably take the non-autonomous type of development, involving an organizer reaction, as typical, differing from mosaic development only in the fact that the mechanism of the process is revealed by the accident that a diffusion of an active substance from place to place is involved.

The reaction between an organizer and competent tissue is not a simple quantitative one, in which the result produced is proportional to the intensity or duration of the reaction. It is rather a reaction in which a choice is taken between a restricted number of alternative modes of development. Thus the primary organizer of the amphibian egg determines the competent ectoderm on which it acts to become either

epidermis, neural tissue or mesoderm. Each of these alternative modes of development is rather sharply defined, and intermediate types of development occur only rarely, and even then are usually much more close to one of the alternatives than to any of the others. Moreover, one sees evidence of the gradual approximation of an originally intermediate type to one of the standard alternatives; for instance, typical neural tissue will eventually be formed even when the earliest stages of its differentiation have not gone through the normal process of forming a neural plate and groove.

It seems clear that the developmental potentialities of the cells are organized in systems which define certain possible modes of development but exclude others. The possible modes can be regarded as in some sense equilibria.

The potentialities which are concerned in these systems must be dependent on the genes, and it becomes necessary to discuss how genes may be expected to fit into the picture of development which we have arrived at. In the first place, we may note that the vast majority of genes do not appear to determine that development shall proceed along distinct alternative tracks; and one might conclude that the discussion above was invalid in this connexion. But before drawing such a conclusion, one should remember the equilibrium character of the alternatives. The sharpness of the distinction between them can only be accounted for if each mode is the result of complex interactions between many component processes, which are adjusted to one another in such a way that only certain combinations are workable. Such a system could hardly arise by chance; its explanation must be sought in the theory of natural selection. Presumably it is an advantage to an animal to develop sharply distinct types of tissue; certainly most animals seem to do so, though exactly why it should be an advantage is not so clear. But the facts that the alternatives must be considered as resultants of numerous elementary processes, and that they are found throughout the animal kingdom, must indicate that they are the result of natural selection of genotypes as complete systems. Any random change in a genotype, then, such as that produced by a mutant gene, may be expected to disrupt the system of mutual interactions on which the sharpness of the alternative modes of development is based. It is therefore not surprising that the majority of gene effects involve a blurring of the clean-cut categories of the normal adult. Malformed tissues, such as forked or singed bristles, and quantitative variations such as bobbed, represent disturbances of carefully evolved equilibria.

There are some genes which, without disrupting the system of alternatives, cause changes to take place within it. The clearest examples, perhaps, are the genes which have been said to bring about hereditary homoeosis. The gene aristopedia in *Drosophila*, for instance, causes the imaginal bud of the antenna to enter on a mode of development which should normally be followed by a leg bud. There is no disruption of the character of the leg-developmental path; it remains as it were one of the standard parts in the developmental symphony; the only change is that it is played by the wrong member of the orchestra. The fact that the leg-like organ which is produced by the antennal bud is formed by the same processes as is the normal leg is indicated by its behaviour under the influence of genes which affect the legs. In *Drosophila*, the normal number of tarsal joints is five, but this is reduced to four in flies homozygous for the genes dachs, approximated and four-jointed. These genes also affect the antennal leg, reducing its length and number of segments, whereas they have no effect on the antenna in non-aristopedia flies. Even some very minor leg effects are reflected in the antennal leg; eyeless-dominant causes a distortion of the segmentation in the proximal part of the tarsus, and produces the same effect on the antennal legs of aristopedia. On the other hand, there are some minor effects produced in true legs which cannot be found in antennal legs. Thus approximated not only reduces the number of segments to four but causes the penultimate segment to be short and swollen. No such effect is found in the leg-like antenna, perhaps because that organ is not long enough for the full segmentation to occur.

Not only is the antennal leg mode of development under the control of leg genes, but it is out of control of antennal genes. Thus thread affects the antenna by removing the side branches from the arista and shortening the axis; but it has no effect on aristopedia antennae. There are, however, some genes which affect both types of development. Thus a mutant dachous-38*k* stunts the development of many parts of the fly, and reduces the size of the antennae both in aristopedia and non-aristopedia flies, though probably somewhat more drastically in the former. Similarly, one of the effects of eyeless-dominant is to cause the comparatively frequent formation of double antennae, and this again may occur both to normal and leg-like antennae.

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WALKER, J.C. ***Disease Resistance in Crucifers***

The problem of disease resistance in the improvement of crucifers through plant breeding is to be discussed. The greatest advances have been made with the yellows disease, important so far chiefly in the U.S.A. The

causal fungus, *Fusarium conglutinans* Wr., is a vascular parasite, which persists indefinitely in the soil. As a pathogen it is confined to the cabbage group (*Brassica oleracea* L.) and it is apparently constant in its selective pathogenicity within that species. Thus variability in host resistance can be dealt with more confidently than with a more variable parasite. In improvement of the cabbage tribe, however, confusion between types of resistance, genotypically different, but phenotypically similar under certain environal conditions, may retard progress in breeding for this character. The highest type of resistance is fortunately due to a single gene, dominant to others which govern various lesser degrees of immunity down to extreme susceptibility. The regulation of soil temperature during testing has been shown to be the simplest and safest method of separating out individuals carrying the gene for high-type resistance either in the homozygous or heterozygous condition, from those in which only genes for intermediate degrees of resistance occur.

In the U.S.A. clubroot (*Plasmodiophora brassicae* Wor.) is important on *Brassica oleracea* L. but minor on turnip (*B. rapa* L.) and rutabaga (*B. napobrassicae* Mill.). This seems to be due to the resistance of most varieties of the last two species. Collections of this organism from various parts of the country exhibit similar pathogenic selectivity. Certain varieties of turnip and rutabaga reported to be susceptible in Europe are immune in U.S.A. This indicates existence of physiologic races of this parasite, which fact must be considered in breeding for resistance.

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WARD, A.H. and CAMPBELL, J.T. ***The Evaluation of Dairy Sires in New Zealand***

Local groups of members are combined into herd testing associations licensed by a central Herd Recording Council which fixes the conditions for recording generally. One condition is that copies of all records must be lodged with the central office and on this large material (250,000 cows) the present report is based. Milk is paid for on a butter-fat basis so that the records are chiefly concerned with butter-fat rather than milk production.

SIRE SURVEY WORK

All cows in a herd must be tested. Preliminary, intermediate and final surveys of a sire's daughters are issued at yearly intervals. At each stage, the survey takes all available lactations into account. The only corrections made are for age in 2 and 3-year-old cows and for very abnormal seasons. Lactations of less than 200 days and portions in excess of 320 days are excluded. Dam's production is estimated from all available records. Surveys are in graph form without any type of sire index.

THE VALUE OF SIRE SURVEYS

Most sire indices involve the assumption of linear regression of daughter's on dam's yield. The magnitude of the implied regression varies among indices, and to determine which approximate most closely to actual coefficients, these have been calculated for forty-one final surveys. The values obtained vary from +0·44 (thirty-one daughter-dam pairs) to −0·32 (seventeen pairs), the general average within sires being +0·14 (significant). Classifying the surveys according to the number of pairs available showed that the value of the coefficient rose from nil with only 10–14 pairs, to +0·19 with thirty-one or more pairs. No single index is likely to give accurate predictions but the daughter mean index (regression 0) seems to fit the facts closer than the parent intermediate index (regression +0·5).

The use of a series of production records as against single records is discussed, and the importance of defining producing qualities on a broader basis than that of a single lactation record per cow. Because sire survey results express the qualities actually being transmitted to the offspring, they form a more reliable guide to selection than production records of the dams. Superior production records are in most cases only a limited indication of the actual breeding superiority of a dam.

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WEINSTEIN, A. ***The Interrelations of Genetic Functions***

In order to test various possibilities as to the arrangement of chromatids and the mechanism of crossing-over, it is desirable to calculate as many genetic functions as possible whose numerical values vary according to the arrangement and mechanism presupposed. The frequencies of chromosome segments having specified boundaries and specified numbers of exchanges will yield such functions. The recombination ratio, inclusive coincidence, select coincidence, homozygosis and heterozygosis in non-disjunction and in attached *X*'s, can be expressed in terms of segment frequencies, and still other functions are possible. The kind of function depends on (1) whether we deal with segments of single chromatids, pairs of chromatids, or tetrads; (2) the boundaries of the segments; and (3) the number of exchanges within the segments.

A boundary may be defined precisely or (where it is an exchange in a nodal region) within limits. If one boundary is defined approximately, the frequencies of such segments can be compared with one another if they are divided by the length of the nodal region; if both boundaries are defined approximately, the frequencies are comparable with one another if they are divided by the respective products of the nodal regions, as is done in coincidence.

Each type of function can be calculated either for all the data or for part only. The part may include tetrads or chromatids of certain ranks; or those that are crossovers, or non-crossovers, in certain regions.

A function can be calculated for map distances based on frequency of crossing-over, on mutation frequency, or on cytological length in ordinary or in salivary chromosomes.

Calculations based on all the published breeding experiments in *Drosophila* and on a larger amount of unpublished data show, among other things, that occurrence and recurrence of crossing-over between homologous strands are random; that exchanges between sister strands either do not occur or do not interfere with exchanges between homologous strands; that as distance increases, inclusive coincidence increases to and remains at 1·00 while select coincidence first increases and then decreases—that is, there is a modal length of internode. There is agreement between these conclusions and cytological studies of chromatid coiling and chiasma frequency in other species.

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WHITE, M.J.D. ***Chromosomal Evolution and the Mechanism of Meiosis in Praying Mantids***

An investigation of meiosis in eleven species of Mantids has revealed a number of interesting facts. In the genera *Ameles*, *Iris*, *Acontiothespis*, *Empusa*, *Gongylus*, *Miomantis* and *Callimantis* there is an *XO*: *XX* sex-chromosome mechanism, the *X* being a V-shaped chromosome. The following genera, however, possess an X_1X_2Y: $X_1X_1X_2X_2$ mechanism: *Mantis*,* *Tenodera*, *Paratenodera*, *Stagmomantis*,* *Hierodula** and *Sphodromantis*. These genera are so close to one another from the taxonomic point of view that it is probable that the X_1X_2Y mechanism arose in a single ancestral species and was transmitted to the genera which evolved from that species. The mechanism could have arisen in the first place by a mutual translocation between one arm of a V-shaped *X*-chromosome and one arm of a V-shaped autosome.

* These genera were investigated by previous workers, and have not been studied by the present author.

The *Y*-chromosome in these X_1X_2Y genera is thus an autosome, which as a result of the translocation has become limited to the male line. It varies in size and in the proportions of the two arms in the different genera.

The X_1X_2Y mechanism appears to be an "inefficient" one, since a considerable amount of non-disjunction of the sex chromosomes takes place in *Paratenodera*, *Tenodera* and *Sphodromantis*.

In all Mantids the meiotic mechanism is of a peculiar type in the male; the usual diplotene and diakinesis stages are omitted, the transition from pachytene to metaphase taking place directly. In *Callimantis* there is no evidence that chiasmata are ever formed; in the other genera the shapes of the bivalents at metaphase suggest that crossing-over may have occurred earlier, but there is no conclusive cytological evidence.

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WHITE, O.E. ***Genes, Species, Variability and Plant Breeding***

From a plant-breeding standpoint, the kinds and causes of variability are of the utmost practical importance. A classification of these in relation to plant breeding is presented and discussed, with examples of their practical applications. Genes are unstable or relatively stable. Gene types appear to differ in the number of their possible allelic changes. Species, as composites of genes, are limited in the direction, extent and kind of their variability by the types of genes they have. Some genes are widely distributed, others are rare. Investigations at the Blandy Experimental Farm indicate species are stable and unstable, depending in part on the stability or instability of their genes. Stable species are exemplified by *Asparagus officinalis*, *Convallaria majalis*, *Ginkgo biloba*, *Vinca rosea*, *Lathyrus latifolius*, *Vinca minor* and *Alyssum maritimum*. Examples of unstable species are *Ricinus communis*, *Zea mays*, *Acer palmatum*, *Thuja occidentalis*, and *Lathyrus odoratus*. With the possible exception of *Zea mays*, none of these is a hybrid in any ordinary sense.

Modern plant-breeding possibilities are discussed from the standpoint of the use of such tools as colchicine, growth-promoting substances, radium, X-rays, centrifuging, temperature, seed aging, and others, together with such techniques as crossing of phenotypically similar different geographical races, use of bees, use of high chromosome pistillate forms for effecting difficult crosses, induction of polyploidy for overcoming sterility, and artificial incubation of weak hybrid embryos.

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WHITING, ANNA R. ***Susceptibility to X-rays of Meiotic Stages in Eggs of*** **Habrobracon**

I. When females of *Habrobracon* are irradiated (2500 r.) and not mated, oöcytes in different stages of meiosis at time of treatment may subsequently either (*a*) degenerate within the ovary, or (*b*) be laid and die before maturity, or (*c*) develop into adults.

(*a*) Degeneration within the ovary is positively correlated with degree of dependence of oöcytes upon accompanying cells (nurse and follicle). Uterine oöcytes show none, oldest oöcytes with nurse and follicle cells, newly differentiated oöcytes and youngest oöcytes with nurse and follicle cells show it in increasing amount.

(*b*) Death of eggs laid which may occur at any stage of development is correlated with the chromatin conditions of the oöcytes themselves at time of treatment as follows:

(1) Eggs which were in first meiotic metaphase fail to hatch.

(2) Eggs which were in latest prophase (diakinesis) hatch but fail to mature.

(3) Eggs which were newly differentiated oöcytes (pre-leptotene) have a high mortality rate (69·6%) and a large percentage dies as larvae.

(4) Younger oöcytes with nurse and follicle cells (early prophase) are most resistant with the exception of

(5) Oldest oöcytes with nurse and follicle cells (late prophase with diffuse chromatin), which have lowest mortality of all.

(*c*) The highest percentage of adults comes from oöcytes which were in late prophase (chromatin diffuse) at time of treatment, no adults from uterine eggs (chromatin condensed). The former were entirely independent of other cells at time of irradiation, the latter almost so. Results must, therefore, be dependent upon primary or direct influence of irradiation upon these oöcytes themselves.

II. The descendants of cells which were oögonia at time of irradiation of females are very few for oögonia and badly injured, perhaps because of their mitotic activity. Mortality of those laid is about midway between lowest and highest of oöcytes.

III. Responses are similar but less extreme for lower dosages (212, 425, 850, 1275 r.).

IV. Ovaries immediately after treatment (2500 r.) show occasional groups of pycnotic nurse cells.

Ovaries five days after treatment (2500 r.) show vacuolated oöcytes, pycnotic nurse cells, oöcytes with follicle layer broken and oöplasm protruding, empty ovarioles, vacuolated oögonial regions and uteri filled with degenerating eggs and nurse cells.

V. Eggs treated (2500 r.) while in the uterus and subsequently incubated for four hours show cleavage in 64·1%, although all would have failed to mature.

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WHITING, P.W. ***The Cytogenetics of Sex-determination***

Cytogenetic work with higher plants has been concerned relatively little with sex, for most Spermatophytes have hermaphroditic flowers or are monoecious, sex-differentiation being developmental rather than genetic. Among the dioecious and trioecious species scattered in various families, genetic studies have been made by means of sex-linked genes and in some cases visible chromosomal differences have been recorded. Sex intergrades appear in great variety, especially after species crosses, and the normal sex-determining mechanism may be genically unbalanced and often accompanied by polyploidy. Environmental conditions play a part in shifting sex type, and a cytoplasmic factor has been postulated to explain difference in reciprocal crosses.

Dioecism occurs in many of the moss plants in which sex chromosomes have been observed and sex-linked traits studied. Polyploid gametophytes have been produced with resulting sex intergrades.

In the higher animals dioecism is the rule with sex intergradation as an abnormality. Owing to relative rate and time of differentiation of parts with a developmental turning-point, it is usually possible to classify non-mosaic sex intergrades as male or as female intersexes with complete sex-reversal as a limit (*Lymantria*), but this condition grades into hermaphroditism (*Drosophila virilis*) comparable to normal hermaphroditism of lower forms in having male and female structures developed simultaneously and retained. Sex mosaics are usually gynanders, but mosaics of sexually different types of male tissue may occur showing phenotypic feminization (complementary sex determination in *Habrobracon*).

Chromosomal sex difference, when visible, consists in less chromatin, or at least less euchromatin, in one sex than in the other. Sex chromosomes have been supposed to occur even when the members of each pair appear equal. The digametic sex has been identified by sex-linkage or has been assumed by comparison with related species. Morphologic series have been made with decreasing size of Y relative to X, and ending in absence of Y altogether. Male haploidy was presumably derived by loss not only of Y, but of one set of autosomes also. Thus the $X+A$ set of the male was supposed merely doubled in the female, $2X+2A$. This theory encounters difficulties as regards genic balance and it has been shown for

Habrobracon that sex-determination is complementary: females are $X+Y+2A$, normal haploid males may be $Y+A$ as well as $X+A$, while diploid males occur, $2Y+2A$ and $2X+2A$. It will be of much interest to determine whether this complementary scheme is general for Hymenoptera and to be extended to other invertebrate groups with haploid males.

By utilizing mutant factors or by selection it has been possible to reverse the type of sex determination as from the digametic male to the digametic female in *Drosophila* and fishes. Reversal is more frequently incomplete so that sex intergrades result.

Sex determination is usually polygenic, but the different genes are normally bound together by lack of crossing-over in the digametic sex. Thus production of sex intergrades in nature is avoided except in race crosses. Linkage and crossing-over of the sex "gene" with other genes (as with fused in *Habrobracon*) have been studied in forms with highly differentiated sexes, but thorough analysis of chromosome fragments in *Drosophila*, especially by the use of triploids, reveals no one locus primarily concerned with sex.

Sex determination known to be monogenic has been produced experimentally as in dioecious maize. In several groups of fungi, the sex-differentiating factor has been treated as a single gene pair, + and −, and its linkage relationships have been studied (especially by Lindegren in *Neurospora*).

In general two sexes, ♂ and ♀ or + and −, seem to have been enough to satisfy most conditions, but in Basidiomycetes, Kniep found four different thallus types, *AB*, *Ab*, *aB*, *ab*, with zygote-forming reaction taking place only between *AB* and *ab*, or between *Ab* and *aB*.

A persistent cytoplasmic factor with sex tendency different from that in the chromosomes has been postulated for Hymenoptera, *Lymantria*, mosses, *Streptocarpus* and other forms. Further investigation has shown this unnecessary for some at least of these cases. Transitory maternal influence, Dauer-modifications and *Y*-chromosomes in female digamety should all be considered here as alternatives.

Initial surroundings of the embryo have been assumed for sex-determination in Hymenoptera, but these, like the cytoplasmic factor with male tendency, are now not needed.

Selective fertilization has been many times invoked and later discarded. In the sense of anisogamy, species specificity or differential pollen-tube growth, it is taken for granted. Even differential maturation of the egg, of doubtful application in some cases and now discarded for *Habrobracon*, seems well-established for others, either cytologically or by breeding test, and should be given careful consideration in all puzzling cases when eggs are of two types, either karyologic or in gross size or storage content (*Dinophilus*, hybrid doves).

Wide disturbance of the "normal" sex ratio with unisexual broods as a limit may be due either to sex reversal (extreme weak and strong race-crosses in *Lymantria*) or to some deviation from the usual random mechanism governing the immediate karyologic cause of sex (parthenogenesis: arrenotoky, thelytoky in Hymenoptera, aphids, etc.) (genotype of mother: arrenogeny, thelygeny in *Trichoniscus* and *Sciara*) (genotype of father: thelygeny in *Drosophila pseudoobscura*).

Finally the case of the dipteran *Sciara* with sex-determining chromosome elimination in development appears thus far unique. Aside from chromosomal elimination causing gynandrism as in *Drosophila*, *Sciara* is the only instance of metagamic karyologic sex determination thus far reported. This highly unorthodox, yet clearly demonstrated example should serve as a suggestion to those examining other forms. Perhaps it may be found that members of some totally unrelated family, some vertebrate or even some dioecious plant, has also in its evolutionary history, stumbled upon the trick of regular chromosomal elimination in cleavage as a means of maintaining sex disparity. Since this appears to be an effective method, can *Sciara* be the only genus that has adopted it?

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WHITING, P.W. ***Sex-determination in*** **Habrobracon**

The earlier view of male haploidy, female diploidy, was unsatisfactory from the point of view of genic balance and was shown inadequate by demonstration, both genetic (1925) and cytologic (1935), of the existence of diploid males. Close-crossed females have since 1924 been known to produce biparental (diploid) sons, fewer daughters and a great excess of non-hatchable eggs. Sex determination was shown (1933) to be complementary. Females (diploid) are digametic, *xa*/*xb*: normal males (haploid) are of two types, *xa* and *xb*: while biparental males (diploid) are homozygous for sex, *xa*/*xa* and *xb*/*xb*. Differential mortality was postulated (1933) to explain excess bad eggs and low numbers of diploid males from close-crossing. Differential maturation of the egg seemed to explain (1933) lack of biparental males and normal egg hatchability in outcrosses. A multiple-factor hypothesis (1935) for the outcross data, alternative to differential maturation, seems not to fit the pedigrees, since the gene *fused*, fu (antennae and tarsi), always shows sex-linkage on inbreeding

after wide crosses unless selection is kept rigidly against production of biparental males. Failure of apparent sex-linkage of *fused* in outcrosses precludes differential maturation. Pedigrees now being derived indicate a series of multiple alleles, of which heterozygosis for any two results in a female-producing zygote while homozygosis determines potential male production but low egg hatchability. Thus zygotes from a close-cross, ♀ *xa/xb* by ♂ *xa*, will be females, *xa/xb*, and potential but highly inviable diploid males, *xa/xa*, while zygotes from an outcross, ♀ *xa/xb* by ♂ *xc*, will all be female-producing, *xa/xc* and *xb/xc*. Any two inbred stocks may be related, both *xa/xb*, unrelated, *xa/xb* and *xc/xd*, or half-related, *xa/xb* and *xa/xc*. Half of the crosses between half-related stocks will be outcrosses and half will be close-crosses.

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WILLIAMS, R.D. ***Incompatibility Alleles in* Trifolium pratense *L.; their Frequency and Linkage Relationships***

Self- and cross-incompatibility in *Trifolium pratense*, a diploid species with 7*n* chromosomes, are determined by a single series of alleles acting as oppositional factors. Recent studies have demonstrated the presence of numerous S alleles in commercial populations of red clover. Twenty-four plants of English late variety and twenty plants of English broad red variety, taken at random from commercial populations, were found to carry as many as 41 and 37 S alleles respectively. In view of these results it is clear that the total number of incompatibility alleles in red clover must be very large. These results further suggest that certain genes mutate much more frequently than is generally considered to be the case.

The various S alleles exhibit different intensities of reaction. The majority appear to be fully incompatible when present in both pollen and pistils, while others are less incompatible in so far as they are capable under certain conditions of effecting pseudo-fertilization. Fully self-compatible plants carrying the completely dominant S^f allele are very rare. So far, only three fully self-fertile plants have been isolated. Two of these S^fS^a individuals are of recent origin, and are known to have appeared as mutations in crosses between self-incompatible parents.

All the evidence obtained from crosses between self-incompatible and self-compatible plants indicates that the fertility factor (S^f) belongs to the same allelic series as the incompatible factors (S^1, S^2, S^3 etc.). This fact has been further confirmed by results of linkage studies involving S^f and the incompatibility alleles.

The factor S, which is located in linkage group 2, has been shown to be linked with two factors for flower colour and seven factors for chlorophyll deficiency.

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WILSON, G.B. ***Alternative Modes of Inheritance* of *Steel-grey Coat Colour in Rabbits***

Steel-grey coat colour in rabbits is darker than agouti owing to reduction of the yellow pigment and generally to the absence of the intermediate yellow banding on the hair. Steels analysed by other investigators were heterozygous, and in material homozygous for agouti, steel × steel gave black, steel and agouti in the ratio 1: 2: 1. The heterozygous nature of steels from Rex and from Dutch stocks is confirmed by my own results with black, chocolate, blue and even lilac forms in normal-coated, Rex-coated or the Dutch marked series. Each of these steels has coloured fur on the belly.

When, however, steels with white bellies, viz. Flemish (from British stock), were mated together, they gave steels, dilute steels and selfs, dense and dilute, but no agoutis. Steel × steel gave 108 steel, 24 black; 4 blue steel, 2 blue. After deducting those steel × steel matings which produced only steel young (39), the ratio of steels: selfs was 2·81: 1. The selfs proved to be ordinary selfs, recessive to steel and to agouti. Furthermore, the existence of homozygous steel was established, viz.: ♀ Ha 307 produced steels only when mated to heterozygous steel and when mated to self:

	Steel
Steel Ha 307 ♀ × Steel (heteroz.) 4/284 ♂:	13
Steel HA 307 ♀ × Self black 4/376 ♂	10

Homozygous steel was slightly lighter coloured than most of the heterozygous steels. Homozygous steel × self blue gave "greys" which were intermediate between steel and agouti. Similar results were obtained from:

Steel, heteroz. × Agouti: 25 "grey", 2 black.

Whether the agouti was heterozygous for self black, or not, did not appear to affect the colour of the "greys".

Thus, it was seen that the introduction of agouti tended to increase the amount of yellow pigment and converted steel into a somewhat intermediate "grey":

	Steel	Black	Blue steel	Blue
Blue steel 5/022 ♀ × steel 4/284 ♂	9	4	12	2

The steel classes thus produced were of a yellowish shade, and so also were blue steels out of the blue steel × self blue. The quantitative presence of yellow was not so distinctive in the dilute, as in the dense pigmented steel.

To sum up, steel when heterozygous for ordinary black was generally dark steel; homozygous steel was slightly lighter steel; steel × agouti gave "grey", intermediate in appearance between steel and agouti. The conclusions reached from these results are that (1) the existence of homozygous steel, with a white belly, has been established; and (2) selfs extracted from this form of steel behave as ordinary black, or other, selfs.

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WINGE, Ö. ***On Inconstancy in Single-cell Cultures of Micro-organisms owing to Segregation and on Hybridization in Yeast***

The classical method of producing pure cultures of micro-organisms is that of starting with a single cell. This was the aim of the various methods invented particularly by Lister, Emil Chr. Hansen, and Robert Koch during the years 1878–83 for bacteria and yeasts. It was regarded as a matter of course that the single-cell culture was bound to be absolutely pure and homogeneous.

We have, however, learnt from genetics that certain cells are haploid and certain others are diploid, and that both phases are present in the normal life cycle of most organisms. Furthermore, the geneticist has often experienced that diploid organisms, and consequently also the cells which form them, may be heterozygous. Now the possibility arises that the single bacteria cell or yeast cell may be of diploid and possibly heterozygous nature and that it may perhaps segregate out new types.

It is usual in higher organisms of plants and animals that the phases in which the organism appears unicellular (egg-cells, sperm-cells) are the haplophases. Micro-organisms, on the other hand, may appear unicellular during the whole of their cycle of development.

Spore-forming types are found both in bacteria and yeasts, and since the spores usually are haploid in higher cryptogams, being formed during the reduction division, there is a possibility that bacteria spores are formed by reduction division, too, as also there was a definite probability of yeast spores being formed by reduction division, as otherwise generally assumed.

Experiments with isolation and cultivation of single spores of *Saccharomyces* species show distinctly that several yeast types are segregated out from one ascus. The single vegetative yeast cell is diploid and usually heterozygous in *Saccharomyces*. Consequently, there may be segregated out types of yeast deviating considerably both morphologically and physiologically from the original yeast, even when a single cell is used at the start, if the yeast gets an opportunity of forming spores. The classical doctrine that unicellular cultures are constant is therefore incorrect so far as the species of *Saccharomyces* are concerned. Certainty for constancy is only obtained by starting from a single spore, as homozygous types may then appear.

Saccharomycodes Ludwigii, when cultivated from a single vegetative cell, turned out to be a peculiar, balanced, double heterozygote, **NnLl**. 50% of the asci segregated out the spores **NL** and **nl**, and 50% **Nl** and **nL**. The spores conjugate during germination in the asci and thus the double heterozygosity is maintained.

A few spore isolations in bacteria have not so far led to any segregation of new types.

The fact that the spores of several yeasts conjugate pairwise in germination makes it possible to hybridize yeast species and yeast varieties. Fourteen hybridizations were carried through under the microscope with a micromanipulator, and several species hybrids and one intergeneric hybrid was thus produced.

By this technique an unlimited number of new yeast types may be produced, while it has so far been impossible to produce a new yeast experimentally. This opens up a new road for rational breeding work with yeast. The yeast hybrids show dominance for the presence of the enzymes saccharase, raffinase, and melibase. A new baking yeast produced by hybridization has proved valuable in practical yeast manufacturing.

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WINTERS, L.M. ***Records of Performance for Meat Animals***

In order that a record of performance be useful it must be usable, for if breeders find the method too complicated, then it will have served no purpose. To be effective a record of performance must identify the factors of performance which have the greatest bearings on profit. In beef animals these factors are economy of gains and suitability of the animals for market purposes. They appear to be of about equal importance in their effects on profit. Economy of gain can be obtained through individual feeding, but that is expensive. Fortunately there is a close correlation between rate of gain and economy of gain; it is

therefore proposed to use rate of gain as an indicator of economy of gain.

In sheep a ewe's performance is calculated in terms of pounds of product, wool and lamb, per unit of feed cost. Feed costs are calculated in terms of maintenance requirements. In the calculation of maintenance requirements it is recognized that maintenance requirements do increase in direct proportion to increased body weight. It is necessary that standard ages be used for time of weaning and time of weighing out of the project.

In swine the factors of chief concern are (1) size of litter raised, (2) feed per 100 lb. gain, and (3) final carcass value. Since environmental factors cause many early death losses, a record should be kept of pigs farrowed alive and pigs weaned. Feed required per 100 lb. of gain is closely correlated with rate of gain; hence it is recommended that rate of gain be taken as a measure of feed lot efficiency. Since an animal cannot be slaughtered and yet retained for breeding purposes, it is suggested that live animal form be used as an indicator of carcass value.

It is proposed that in the selection of breeding stock all the factors affecting the animal's value be taken into consideration individually rather than collectively because a serious defect in any one is enough to make the animal useless in a breeding herd.

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WOODWORTH, C.M. ***Inhibiting Factors in Soy Beans***

Studies on the genetics of soy beans have revealed several instances of the action of inhibiting factors. These are briefly described as follows:

Glabrousness v. pubescence. Dominant glabrous ($P_1P_1P_2P_2$) × recessive glabrous ($p_1p_1p_2p_2$) gives glabrous in F_1, and thirteen glabrous to three pubescent in F_2. Gene P_1 behaves as an inhibiting factor suppressing the action of gene P_2 for pubescence. P_1 also inhibits growth since the glabrous segregates are smaller and lower in yield than the pubescent segregates. p_2 may be said to inhibit growth also since the double recessive is a very small, weak type and always appears as such even as a segregate in crosses. The recessive glabrous type is much smaller and weaker than the dominant glabrous type.

Pigment on seed coat. Multiple allelomorphic series: I–i^h–i^k–i. Factor I inhibits black and brown colours in the seed coat. Factor i^h permits black or brown only in the hilum, and i^k permits black or brown to spread out from the hilum over the sides of the seed in a saddle pattern. Self-black or self-brown beans possess factor i.

Pubescence colour. Normally, tawny pubescence (T_1) is dominant to grey (t_1). However, a grey pubescent type crossed with ordinary grey (t_1) gave grey in F_1 and what appeared to be a 13 grey to 3 tawny ratio in F_2. These results were explained by assuming an inhibitor (T_2) which prevents T_1 from expressing itself. However, it does not prevent complementary action of T_1 with R to produce black pigment in seed coat.

Determinate v. indeterminate growth habit. Indeterminate growth habit (Dt) ordinarily is dominant to determinate (dt). However, in a cross involving different parental types, the reverse was the case, and in F_2 a ratio of approximately 13 determinate to 3 indeterminate was obtained. It appears that one determinate type is therefore recessive and the other is dominant to the indeterminate type. The latter may be due to a factor which inhibits Dt from expressing itself.

Seed size. In crosses between the wild soy bean (*Soja ussuriensis*) and the domestic types, small seed size of the wild is partially dominant to large seed size. This may be explained by assuming that the wild soy bean carries inhibiting factors for seed size. Since small seed size of the wild parent is not recovered easily in F_2 or shown by F_1, the wild parent may carry some dominant, some partially dominant or partially dominant inhibiting factors for seed size.

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WOOLLEY, G.W. ***The Effect of Male Secretions upon Tumour Incidence in Mice***

Tumour incidence in a series of female mice joined throughout life to male mice (parabiosis) is presented. In brief the results are that there has been a great reduction, or at least postponement, of mammary tumours following parabiosis. Only one mammary tumour has appeared in the 101 pairs, and this approximately four months beyond the average age for virgin females of this stock.

The question arises as to whether this result is due to the influence of male secretions in the body of the female or to some other influence associated with parabiosis. At present the results indicate that some influence other than that of male secretions is in operation changing the mammary development and probably the tumour incidence in the females of the male-female pairs, since in the animals examined the mammary glands of the females of both the female-female and the male-female pairs were not well developed.

WRIGHT, S. ***A Quantitative Study of the Interactions of the Major Colour Factors of the Guinea-pig***

INTRODUCTION

Animal or plant breeding appears at first sight to be a very crude type of physiological investigation. Yet from one viewpoint it is a rather penetrating method. There is the opportunity of making exactly one or two, or in some cases more replacements of one of the ultimate physiological agents of living matter without any experimental disturbance. A given measurable character may be affected by many such sets of alternative agents, and the quantitative effect of each gene replacement can be studied in a great diversity of different genetic backgrounds, as well as under different environmental conditions. There are, of course, obvious limitations. It is impossible to attain such certainty of interpretation as in reactions carried out with isolated materials in the test-tube. Advance in physiological genetics will require maximum utilization of both methods.

The colours of animals and plants have long been recognized as among the most favourable characters for study of gene physiology, both because of the multiplicity of gene combinations which can be distinguished and because of the probable relative directness of the relations between primary gene action and observed character. I wish to review the results of studies of coat colour in the guinea-pig which have been conducted from this viewpoint.

MEASUREMENT OF PIGMENTATION

The coat colours of the guinea-pig, as of other mammals, fall into two main series, dark (or melanic) colours and yellow (or xanthic) colours. The actual pigments of these series are undoubtedly closely related and all belong to the group known as melanins. In our laboratory, more than 10,000 animals distributed among several hundred different genotypes have been graded at birth, and in many cases later, by means of squares of skin in which the colour of the hair progresses by scarcely perceptible changes from white (grade 0) to intense red (grade 13) in the xanthic series and from white (grade 0) to intense black (grade 21) in the melanic series. There are minor differences in quality within the melanic series, but for the most part these are not great enough to interfere with grading. Our grades were found by Kröning to agree very well with ones which he established.

The set of average grades of the various genotypes establishes the *order* of intensity but does not, of course, measure the relative *quantities* of pigment. If, however, the average quantity in representatives of each grade can be established, it becomes possible to

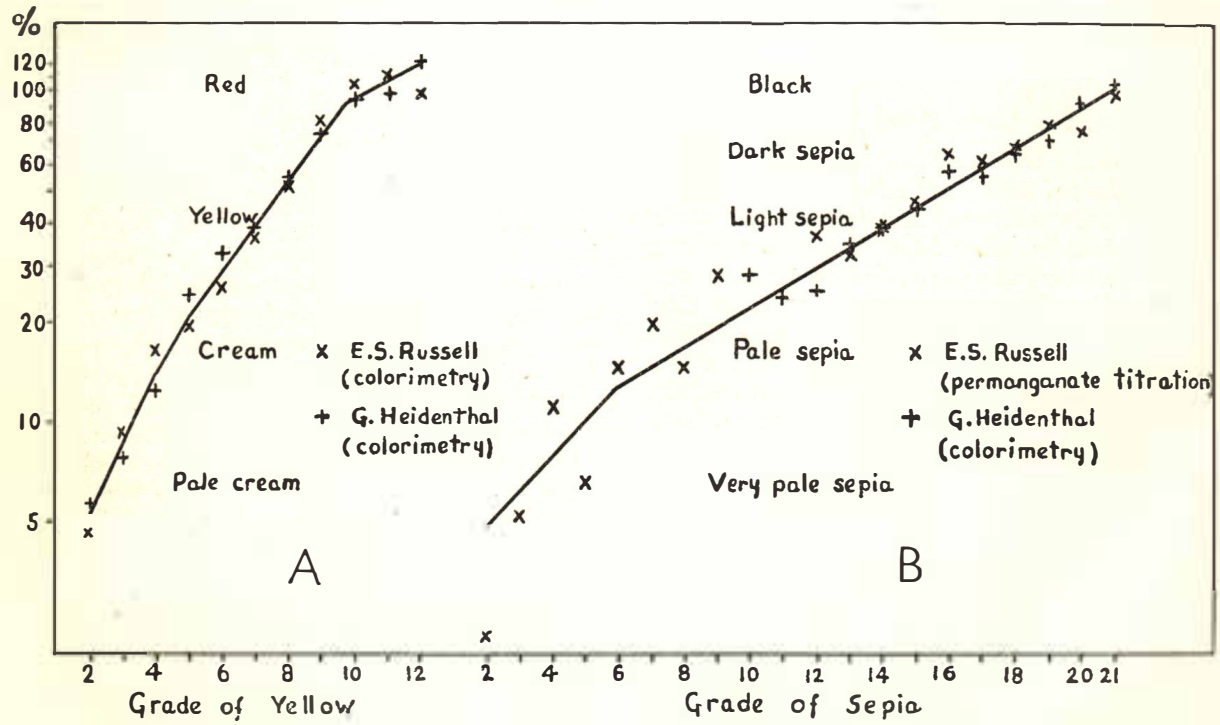


Fig. 1. Amount of pigment by colorimetry or titration with $KMnO_4$ plotted against grade. Intense red (A, left) and intense black (B, right) taken as 100% (E. S. Russell and G. Heidenthal).

transform the grade averages into quantitative averages.

The measurement of quantity of melanin presents various theoretical and practical difficulties. Probably there is no method available at present that can be relied upon completely. In our laboratory we have found excellent agreement between the results of two widely different methods of measuring melanic pigmentation: titration with $KMnO_4$ of pigments extracted from weighed samples of hair by the method developed by Einsele (Dr Elizabeth Russell) and colorimetric comparison of alkaline solutions of similarly extracted pigment (Dr Gertrude Heidenthal). There was fair agreement with weight of pigment in one comparison, although, as in Einsele's results, there was some indication that pigment from lower alleles of the albino series may be slightly lighter in colour per unit weight. Colorimetric measurement of grades of yellow by both Mrs Russell and Miss Heidenthal have given consistent results. Titration with $KMnO_4$ was also tried with yellow. While the results were rather variable they indicated that a typical intense yellow (grade 10) has only about 20% as much reducing capacity per unit weight of hair as an intense black (grade 21).

Some of the results are shown in Fig. 1 A, B, where the logarithms of the relative colorimetric values are plotted against the grades. A succession of straight lines was fitted by least squares to the weighted averages in each case and used as a basis for transformation of the grade averages.

Physiology of pigmentation

It is probable from somatic mutations (Wright and Eaton, 1926; Dunn, 1934) that the major colour genes of mammals act locally. We are thus dealing with intracellular rather than organismic physiology.

It has been well established that the melanins come from tyrosin or related substances (such as dopa) under the influence of oxidative enzymes. Danneel and Schaumann seem to have cleared up difficulties with earlier studies of skin extracts. They have devised means of separating dopa oxidase from inhibiting substances present in extracts from black rabbits. Danneel has given evidence for a chain of three processes: first, one that is suppressed by X-rays and second the anoxidative formation of dopa oxidase, occurring under continuous high temperatures (over 37°) in intense rabbits (C) but only after a period of exposure to temperatures below 33° in Himalayans (c^Hc^H) and failing completely in albinos (cc). His third reaction, resulting in pigment formation, requires oxygen and is inhibited by HCN. The above temperature effect is in harmony with the previous observations of Schultz and others that pigment develops in Himalayan rabbits only in regions of the skin that have been exposed to cold.

Another method of demonstrating the occurrence of dopa oxidase has been from the reaction of frozen sections of skin to buffered solutions of dopa. Schultz and Kröning have found differences among a number of genotypes in rabbits and guinea-pigs by this method. In our laboratory, Dr W. L. Russell has used this method extensively.

Mathematical theory

To make full use of the quantitative determinations of the effects of gene substitution, it is necessary to apply a mathematical theory. This is a hazardous venture in connexion with complex processes of the living cell. Yet it seems better to attempt to use some simple quantitative theory consistently than to restrict oneself to merely verbal reasoning. It is usually easy to suggest a plausible interpretation of any particular interaction, but difficult to appreciate the implications throughout the entire network of reactions unless one introduces numbers.

Pigment is being produced throughout life. While certain processes are irrevocably determined early in development, it appears that the action of most of the genes in which we are interested here, or at least of active products of these, must take place more or less continuously. It will accordingly be assumed that the observed quantities reflect the rates of certain reactions during a phase of flux equilibrium rather than differences in duration or timing of the reactions (Wright, 1929, 1934).

An observed character difference may be at any number of removes in a chain reaction from the causal difference. Moreover, as illustrated in Fig. 2A, it need not be connected by a direct chain at all. A change at one point in the network of interacting processes may decrease or increase production in collateral processes through competition effects. We will assume as short and direct a chain of processes in each case as will suffice, but there is nothing to prevent elaboration if further data make it necessary.

One type of elementary reaction that needs consideration is that of Fig. 2B. An agent, A, whose rate of production $\dot{A}$ is affected by differences in a given gene, interacts with a substrate S to produce the observed product, P, or a precursor. The rate of production, $\dot{P}$, depends jointly on the concentrations (A) and (S) which, under flux equilibrium, depend on the balance between the rates of production $\dot{A}$ and $\dot{S}$ and the rates of dissipation whether in formation of the product $c\,(A)\,(S)$, or otherwise, $b\,(A)$ and $d\,(S)$. The rates of production are related by the equation

$$\dot{P}=\frac{c}{bd}(\dot{S}-\dot{P})\,(\dot{A}-\dot{P}).$$

Fig. 2C represents the case in which the agent is a catalyst, produced in a certain quantity E, a portion of which is free (F) and the rest (B) bound in an intermediate product with the substrate. The equation is the same as in the preceding case on substituting b (E) for $\dot{A}$.

zygotes with an amorph, but as an antimorph in heterozygotes with an allele which produces a more efficient product. Such an allele might be called a mixomorph.

The greatest weakness of the attempt to make physiological deductions from the study of factor

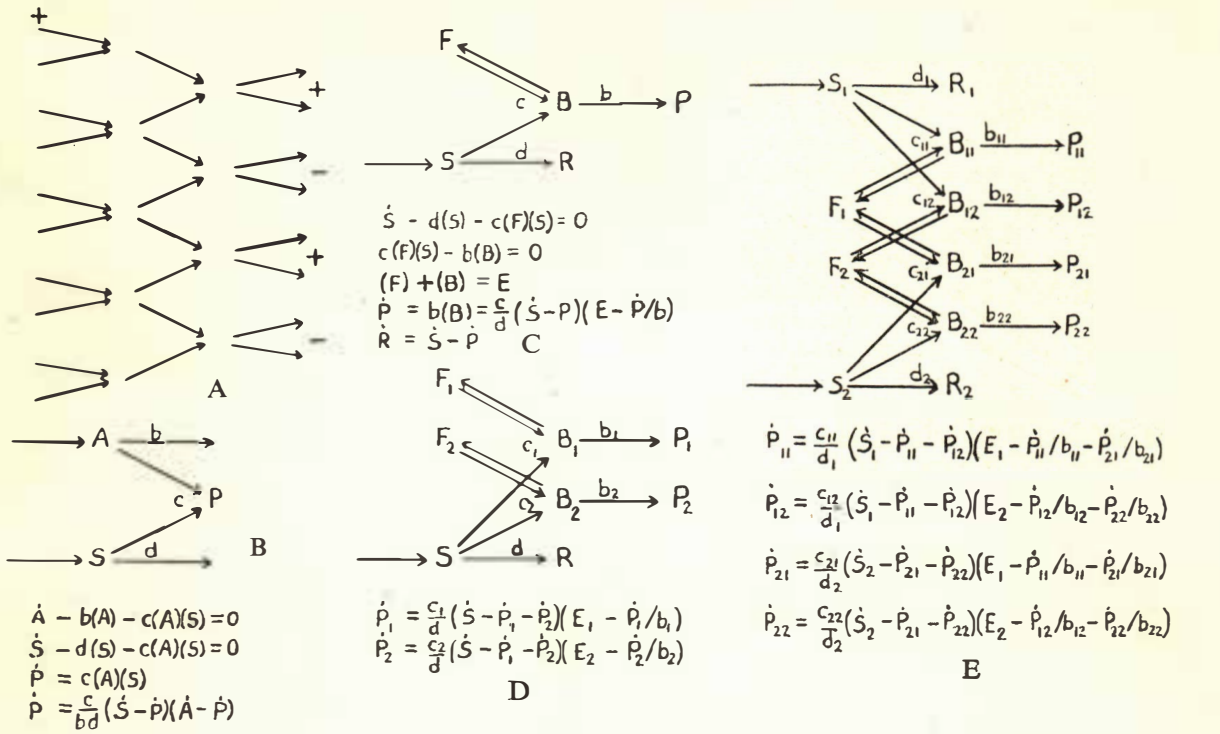


Fig. 2. Reactions under flux equilibrium: A, upper left, illustration of possible indirectness of relation between variation in cause and effect; B, lower left, case of non-catalytic interaction of agent (A) and substrate (S); C, upper middle, case of catalytic action; D, lower middle, case of two catalytic agents; E, right, case of two catalytic agents and two substrates.

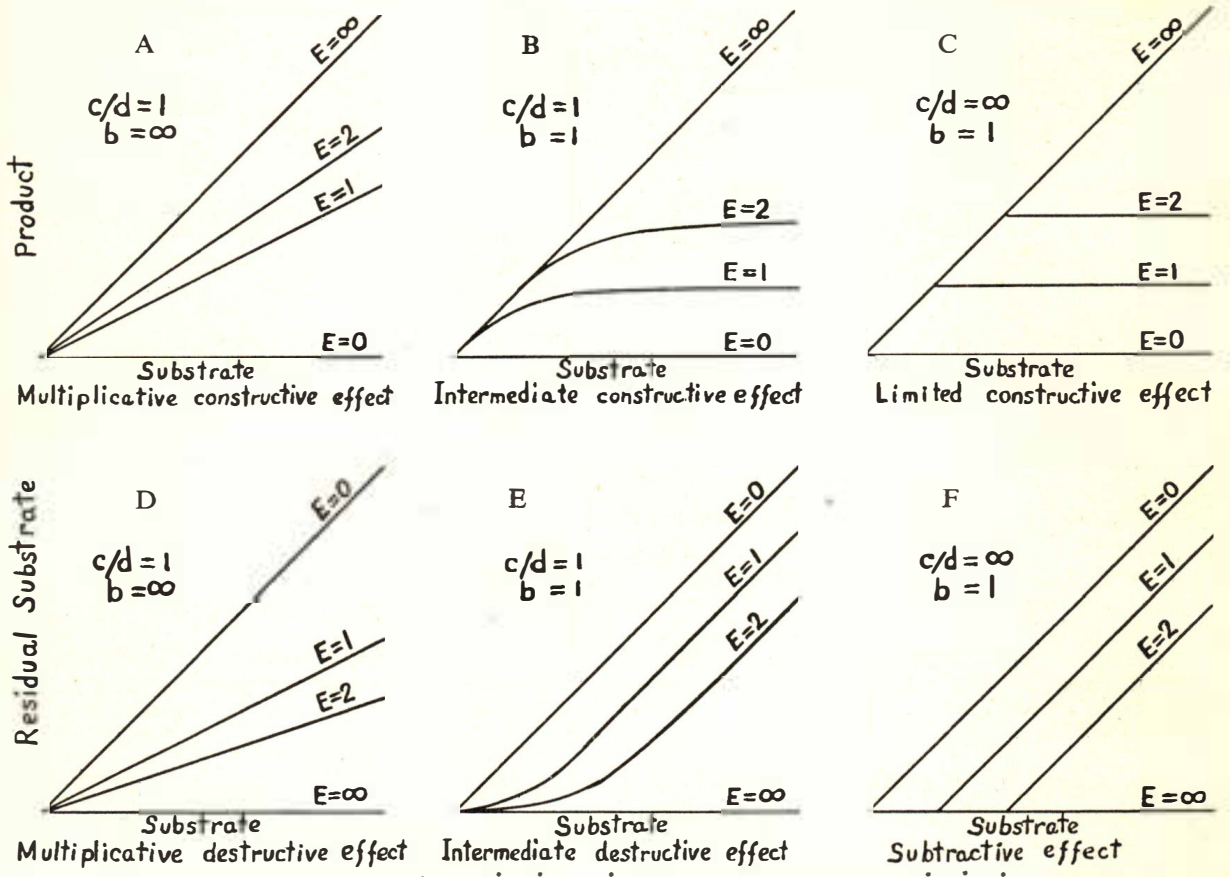
If E is the gene itself, the amount of E is the same for all alleles (with the exception of deficiencies and duplications), but the different alleles may differ in the rate coefficients c and b. Moreover, in this case the products may well differ in specificity in the same sense as the alleles, if as previously suggested (Wright, 1927) production is related to the process by which genes duplicate themselves between cell divisions. Thus products formed equally freely from the substrate (same c and b) may differ in efficiency in relation to the characters actually observed. There is no difficulty on this basis in understanding how certain alleles may, in Muller's terminology, be amorphs ($c=0$), others hypomorphs, others hypermorphs in relation to type; and others antimorphs (P freely formed but with zero efficiency and thus destroying substrate that might otherwise be utilized). An allele that produces freely a product of low efficiency would behave as a hypomorph in heterozygotes with an amorph, but as an antimorph in heterozygotes with an allele which produces a more efficient product. Such an allele might be called a mixomorph.

The greatest weakness of the attempt to make physiological deductions from the study of factor interactions arises from this possibility that gene substitution may bring about not only quantitative differences along a chain of reaction but also transmit differences in specificity. It is possible to dismiss any interaction effect as merely an inexplicable manifestation of specificity, an emergent in the sense of Lloyd Morgan. On the other hand, it is obvious that the greater the number of steps in the reaction chain between gene and product, the less the likelihood that any differences in specificity among alleles will be carried through to the latter, and thus the greater the likelihood that the effects of gene replacement at this point will be purely quantitative. We will treat products as differing merely quantitatively as far as possible.

Fig. 3 A–C is intended to bring out the relation between the rates of production of substrate and of a particular product under the influence of a gene that plays an irreplaceable role as a catalyst. Different

rate coefficients are assumed in this figure. In Fig. 3 B, where both c/d and b are finite, there is an approach to complete dominance of the active phase of the gene over an inactive phase if the substrate is much in defect, practically no dominance if the substrate is in excess, with intermediate degrees of dominance between. Two extreme cases are shown in Fig. 3 A, C. In Fig. 3 A (c/d finite, $b=\infty$), the effect has a destructive effect. Again the gene has a multiplicative effect (in this case in the direction of decreased amounts of product) if c/d is finite, $b=\infty$, while it has a subtractive or threshold effect if $c/d=\infty$, b is finite. In interpretation it is convenient to use the extreme cases as far as possible because of their simplicity.

If alleles differ in the rate constants c and b rather



Rate of formation of product ($\dot{p}=c/d\,(\dot{S}-\dot{P})\,(E-\dot{P}/b)$) and of residual substrate ($\dot{R}=\dot{S}-\dot{P}$) in relation to rate of formation of substrate ($\dot{S}$), amount of enzyme (E) and rate constants c/d and b.

Fig. 3. Relations between substrate and product in reactions brought about by one or two representatives of catalytic agent with various rate onstants. A, B, C, upper row, constructive action; D, E, F, lower row, destructive action.

of the gene is strictly multiplicative, the rate of formation of the product being always a certain multiple of the rate of formation of the substrate $\left(\dot{P}=\frac{cE\dot{S}}{cE+d}\right)$. The degree of dominance $\left(\frac{2cE+d}{2cE+2d}\right)$ is the same for all rates of formation of substrate. In Fig. 3 C ($c/d=\infty$, b finite), there is a ceiling effect; the product depends merely on which is the limiting factor, substrate or gene. Fig. 3 D–F shows the relations between substrate and product where the gene

than in quantity (E) the effects of heterozygosis may become somewhat complicated as indicated in Fig. 2 D. There are further complications if two or more substrates compete for combination with the gene as indicated in Fig. 2 E, the system used in interpreting the effects of the albino series.

The distribution of colour

The colour factors of the guinea-pig may be divided primarily into those that determine the distribution of

colour in the coat irrespective of its kind, and those that determine quality and quantity of colour in the coloured areas.

The factors that determine the common piebald pattern (principal gene S, s) are representatives of the first group. It is generally agreed that there is no dopa reaction whatever in the white areas, but this probably indicates absence of pigment cells rather than mere absence of dopa oxidase.

Melanic differentiation

Fig. 4 shows the quantity of pigment (melanic above, xanthic below) in some of the more important gene combinations. The effects of the compounds of the albino series, arranged in what seems the most significant order, are shown in combination with genes of other series. A condensed tabulation of the quantities of pigment in the more important combinations is given in Table 1.

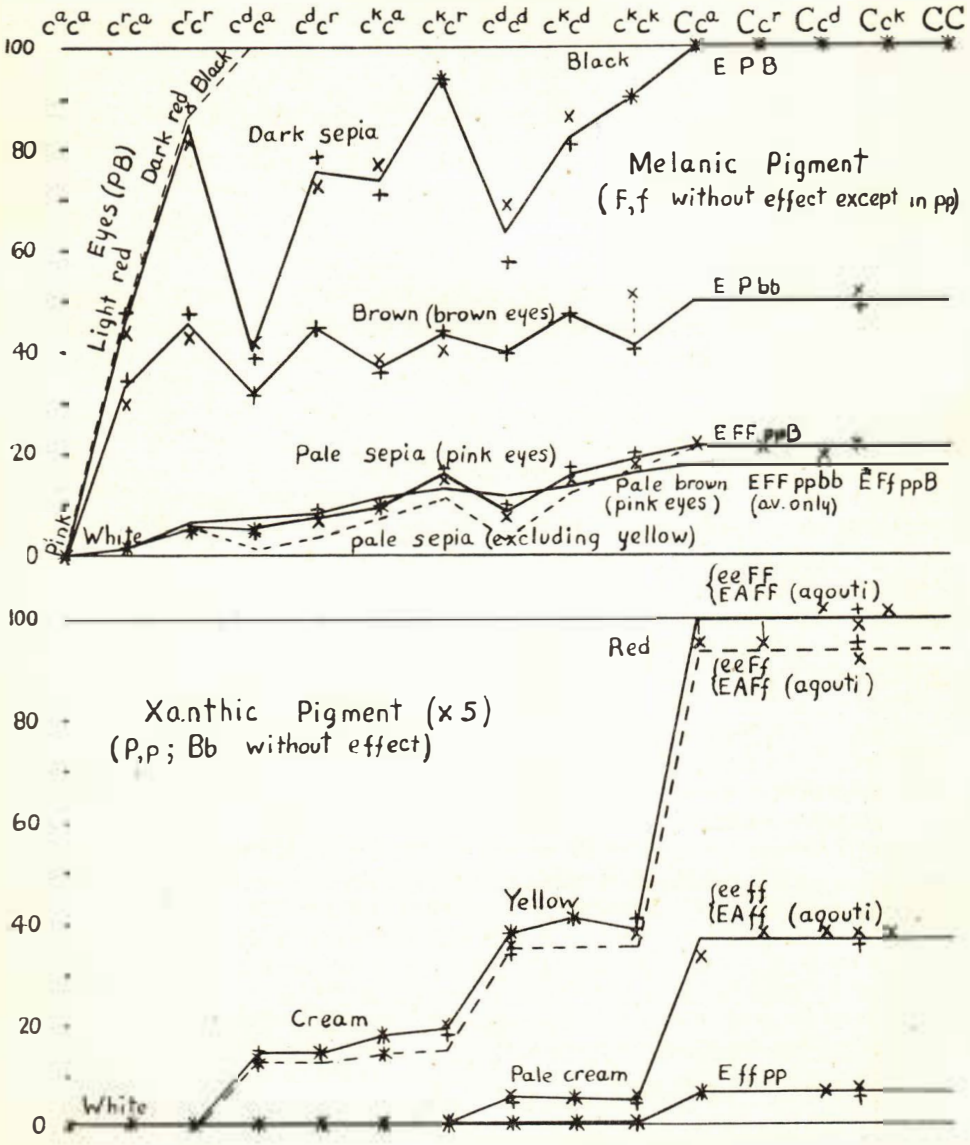


Fig. 4. The average quantities of pigment (by transformation of grades) in various gene combinations. Melanic pigment above. Xanthic pigment below. +, quantities from average grades published in 1927. ×, quantities from average grades during the period 1933 to 1938.

Table 1. *The average concentrations of pigment in the hair of guinea-pigs at birth.*

	Sepia		Brown		Yellow			Eye colour (E, e; F, f without effect)		
	EPFB EPfB	EpFB	EPFb EPfb	EpFb	EpfB Epfb	ePFB ePFB epFB epFb	ePfB ePfb epfB epfb	PB	Pb	pB pb
C-	100	21	50	17	6	100	36	Black	Brown	Pink
c^kc^k	90	18	42	15	0	38	5	Black	Brown	Pink
c^kc^d	82	15	47	13	0	41	5	Black	Brown	Pink
c^dc^d	64	9	40	11	0	38	5	Black	Brown	Pink
c^kc^r	94	14	43	13	0	19	0+	Black	Brown	Pink
c^kc^a	73	9	37	11	0	18	0+	Black	Brown	Pink
c^dc^r	75	7	44	7	0	14	0+	Black	Brown	Pink
c^dc^a	40	5	31	6	0	14	0+	Black	Brown	Pink
c^rc^r	84	5	45	6	0	0	0	Dark red	Dark brown-red	Pink
c^rc^a	46	1	33	1	0	0	0	Light red	Light brown-red	Pink
c^ac^a	0	0	0	0	0	0	0	Pink	Pink	Pink

The sepias and browns are given on a scale in which intense black (EPBC) is 100. The yellows are given on a scale in which intense yellow (eeFFC) is 100. The latter actually has only about 20 % as much capacity for reduction of $KMnO_4$ as intense black. Replacement of aa, assumed above, by A replaces the sepia, brown or yellow of E combinations by the yellow of the corresponding e combinations in a subterminal band in each hair in the e combinations. There is no effect. The averages for the b combinations, especially pb, are based on relatively inadequate numbers.

The most important factors in distinguishing the melanic and xanthic colours are those of the series E, e^p, e. With E present, the entire coat, the eye, and skin tend to exhibit melanic pigmentation. With ee the entire coat (at birth) exhibits only xanthic pigment (if any). There seems to be only melanic pigmentation with ee in the skin although a reduced amount compared with E. The eyes (in ee) are melanic and indistinguishable from those of animals with E. With e^pe^p and e^pe the coat shows a tortoiseshell mixture of the colours found in otherwise similar animals of constitutions E and ee. The yellow area is considerably greater on the average in e^pe than in e^pe^p, although there is much overlap (Chase). Transplantation experiments indicate that the pattern is irreversibly determined early in development (Seevers and Spencer). This process we will call melanic differentiation. It is affected by minor modifiers in tortoiseshells. The most important modifying condition, however, is white spotting. With no white (SS e^pe^p) tortoiseshells characteristically show a mixture of relatively few yellow hairs on a melanic background. In tricolours (ss e^pe^p) there is more yellow, and the melanic and xanthic colours tend to be segregated into distinct spots (Wright, 1917; Chase, 1939). It appears that the same factors that affect the capacity of the primordial pigment cells to reach all parts of the skin also affect their tendency to undergo melanic differentiation.

The characterization of the coat with E present as melanic and with ee as xanthic requires qualification. A small amount of xanthic pigmentation seems to be present in certain combinations mixed with the prevailing melanic pigment (E c^dc^d F ppB yellowish sepia in contrast with E c^rc^r F ppB slaty sepia).

Moreover, certain factors bring out pure xanthic pigmentation in spite of E. Thus agoutis, EA, show xanthic colour (in subterminal bands in the hair) of the same intensity as that shown by otherwise similar animals in which E is replaced by ee. With A^rA^r and A^ra, involving a gene introduced into the guinea-pig from crosses with another species (*Cavia rufescens*), there is a similar pattern except that the extent of yellow on both back and belly is much reduced. With aa there is no such pattern. Genes A and A^r must act *before* there has been any interference of the melanic processes with the xanthic process to account for the full intensity of the xanthic colour.

Pure xanthic pigmentation is also exhibited in the combination E C ff pp. In this case, however, the intensity is much reduced. There is only about 17% as much pigment as in ee C ff pp. It must be concluded that in this case the melanic process is blocked (by simultaneous failure of P and F) *after* it has interfered with the xanthic process.

That the postulated melanic differentiation of the embryonic skin is not an absolute prerequisite for melanic pigmentation is shown by the fact that in hair that is purely xanthic at birth (as in the whole coat of ee) considerable melanic sootiness may appear with age, especially after temporary thinning of the hair with exposure to low temperature). This sootiness is affected by modifiers (such as P, p; B, b) in the same way as the pigment in the areas of melanic differentiation. It is also inhibited subterminally by the agouti factor, A.

The albino series

The albino series plays a fundamental role in the determination of both kinds of pigment. With c^ac^a,

there is no pigment at birth in any combination with other genes (white with pink eyes). The allele **C** determines the highest intensity of pigment found with each combination. It is completely or almost completely dominant over all of the other alleles in all combinations. At one time, the averages indicated considerable incompleteness of dominance in the combination **E** C^a**pp**, but more recent data indicate that this was due to inadequately controlled modifying factors.

There are peculiarities in the effects of intermediate alleles. Only three alleles (**C**, c^{kd}, c^{ra}) are distinguishable in effect on xanthic pigment, resulting in four successive levels with respect to quantity if the compounds are arranged as in Fig. 4. The genotypes ee c^rc^r and **ee** c^rc^a are as white as albinos (**ee** c^ac^a), though differing in eye colour. The four compounds in which either c^k or c^d is heterozygous for either c^r or c^a (ee $c^{kd}c^{ra}$) have from 14 to 19% as much pigment as intense reds (**C**). A slight difference is indeed indicated between c^kc^{ra} and c^dc^{ra}, but this may be due to modifiers. The three compounds represented by $c^{kd}c^{kd}$ are practically indistinguishable with 38 to 41% as much pigment as in **ee C**, and thus more than twice as much as in the heterozygotes $c^{kd}c^{ra}$.

On considering the sepias (**EPB**) in the same order one finds a succession of waves in place of the levels in the yellows. At the level of no yellow, sepia rises from c^ac^a (white) through c^rc^a (46%) to c^rc^r (84% of the pigmentation of black, **C**). With the appearance of yellow in c^dc^a, sepia drops to 40%, rising through c^dc^r (75%) and c^kc^a (73%) to a new high level in c^kc^r (94%), while yellow remains unchanged. With the rise in yellow in c^dc^d, sepia falls to 64%, to rise at this level of yellow through c^kc^d (82%) to c^kc^k (90%).

The melanic pigmentation of the eyes gives a third order. There is no pigmentation in the pink eyes of albinos. In c^rc^a the eyes are much darker but show a strong red reflexion through iris and pupil. They are still darker in c^rc^r, but the pupil still appears red. In c^dc^a and all higher compounds the eyes appear black. Thus c^dc^a has more black in the eyes than c^rc^r but less black in the coat.

In previous papers (Wright, 1916, 1917, 1925, 1927) it has been suggested that the albino series determines a linear series of rates of production or of potencies of a substance necessary for any pigmentation in the order c^a, c^r, c^d, c^k, **C**, and that the irregularities are due to a difference in threshold depending on the presence or absence of **E** product, with competitive interference in the hair follicles but not in the eyes of the xanthic with the melanic process above the threshold at which the former can be formed. The hypothesis that a higher threshold for yellow than black is characteristic of the albino series has been borne out by the later discoveries of similar conditions in rabbits, rats, mice, cats, etc. Some evidence from other cases was adduced for a competition between the xanthic and melanic processes, although no other cases involving the albino series seem to have been described. Difficulties were recognized which have become more obvious on attempting a quantitative interpretation. We will return to these after considering certain other combinations.

Specific modifiers of melanic pigmentation

The replacement of **P** by **pp** greatly reduces the amount of melanic pigment in the coat (**C pp** = 21% of **CP**), the skin, and the eyes (pink), but has no effect whatever on xanthic pigment. The effect is exaggerated in lower compounds, especially in c^rc^r **pp** with only 5% of c^rc^r **P**; and in c^rc^a **pp**, which is sometimes pure white at birth and has only a trace of colour at best. The reduction of c^rc^a **pp** to less than 50% of c^rc^r **pp** is taken to indicate a slight subtraction effect. The order of the grades is different from that with **P** (e.g. c^rc^r **pp** < c^dc^d **pp** but c^rc^r **P** > c^dc^d **P**). This may be due to the presence of considerable xanthic pigment in such compounds as c^dc^d **pp** which is wholly lacking in c^rc^r **pp**. The compounds c^dc^a **pp**, c^dc^r **pp** and c^dc^d **pp** have a very yellowish appearance (in contrast with c^kc^a **pp** and c^rc^r **pp**) and occasionally have approached pure light yellow so closely that a breeding test was necessary to establish the constitution.

The replacement of **B** by **b** has effects which in several ways resemble those due to replacement of **P** by **p**. In both cases melanic pigment is reduced in hair, skin and eyes. In neither case is there any effect on xanthic pigment. There are, however, two important differences. The browns (**E P bb**) appear to differ qualitatively from the dark-eyed sepias (**EPB**), while the pink-eyed sepias (**E ppB**) do not. The higher compounds of the albino series are more alike in browns than in dark-eyed sepias while, as just noted, the reverse is true in the pink-eyed sepias. Thus the ratio c^rc^r to **C** is 84% in dark-eyed sepias, 91% in browns but 25% in pink-eyed sepias. The ratio c^rc^a to c^rc^r is 54% in dark-eyed sepias, 73% in browns and probably less than 25% in pink-eyed sepias, where the quantity in c^rc^a **pp** is too small to measure. Dunn and Einsele have found a similarly slight effect on brown of compounds of the albino series in mice. The double recessive, pink-eyed browns, **E pp bb**, differ qualitatively from the pink-eyed sepias but apparently very little in quantity. Where **E P bb** has about 50% as much pigment as **EPB**, **E pp bb** has about 80% of the intensity of **E ppB**. Among the lower compounds, the grade assigned pink-eyed browns was practically the same as that assigned the corresponding pink-eyed sepias.

These facts can be explained on the hypothesis that the **C** and **P** series affect the quantity of an agent

which acts on a limited melanic substrate according to the intermediate theory, and that the product is completely transformed into sepia if **B** (completely dominant) is present but is transformed into brown according to the intermediate theory if **B** is absent. With **P** present, the substrate is to a considerable extent the limiting factor, and the sepias show a damping of the effects of the higher compounds of the albino series and the browns exhibit a more pronounced damping of this sort. If, however, the quantity of the agent is reduced to only about 5 % of its value by replacing **P** by **pp**, the agent becomes the limiting factor in the main. On this hypothesis the true quantitative relations among the compounds of the albino series are presented more faithfully in the pink-eyed browns and sepias (at least after correcting for a probable late subtractive effect and for the presence of xanthic pigment above c^rc^r) than in black-eyed sepias. The results can also be interpreted on the basis of separate sepia and brown substrates.

The albino series again

It will be convenient here to return to consideration of the irregularities of the albino series. We may distinguish three alternative interpretations of the threshold difference between xanthic and melanic colours: (1) There may be a subtraction from the primary effects of the *compounds*, in the absence of melanic differentiation, which reduces c^rc^a and c^rc^r to white. (2) There may be a subtraction from the primary effects of the separate genes. (3) The difference in threshold may be in the potency of the genes themselves relative to yellow and sepia substrates. Under (1) c^dc^r and c^kc^r should produce more yellow than c^dc^a and c^kc^a, if c^r is higher than c^a in a quantitative series. Since this is not the case, this alternative is eliminated. Under (2) there should be little or no competitive effect of the xanthic c^d reaction with the melanic c^d reaction, since under this hypothesis the genes of the albino series (or their products) combine with **E** product in preference to the inhibiting substance, and with the latter in preference to the xanthic substrate. As for competition between the reactions for utilization of another substance of limited quantity, this sort of competition should be greatest with **C** present and should be negligible with c^d if the effect of c^d is as low relative to **C** as is indicated in the pink-eyed sepias and browns. Since the only evidence for successful competition of yellow with sepia comes in the c^d compounds (the melanic process almost suppressing yellow in the presence of **C**), this alternative must either be ruled out or the reversed effects of c^d and c^r in eye and hair be attributed to specificity rather than to differences in competition. This brings us to the third alternative, viz. that c^r and c^a are specifically unable to act on the xanthic substrate although able, in widely differing degrees, to act on the melanic substrate. In the mathematical theory, it is necessary to postulate increasing values of both rate constants, **c** and **b**, in relation to both substrates, apparently implying four dimensions of variability among alleles. However, the ratio of **c** to **b** may be constant in each case, reducing the number of dimensions to two, which in turn may not be independent. There is no difficulty in assigning values to the constants that will account for the observed differences in order of effect of c^d and c^r in coat and eyes on the hypothesis that there is a yellow process only in the former.

The close similarity if not identity of c^d and c^k in effect on yellow is another difficulty in applying the original hypothesis of a single quantitative order. We will here merely accept this identity with respect to yellow, assigning higher rate constants to c^k in effect on sepia.

The complete or nearly complete dominance of **C** over the other alleles in all combinations, including ones in which the intensities of yellow and sepia are greatly reduced (e.g. ee Cc^a **ff**, **E** Cc^a **ff pp**, **E** Cc^a **FF pp**), implies that **C** (or a product) is in excess relative to its substrate in a reaction *preceding* action of **F** or **P**. We assume that **C** is in excess relative to its immediate substrate while its lower alleles are in defect.

The combinations with F, f

The intensity of yellow is markedly reduced by replacing **FF** by **ff**. There is relatively (but not absolutely) more reduction in $c^{kd}c^{kd}$ than in **C**. In $c^{kd}c^{ra}$, xanthic pigment is almost or wholly lacking. The fact that **F** is not completely dominant over **f** suggests an approach to a multiplicative effect. The data are in fair agreement with such an effect if supplemented by a later small subtractive effect.

This replacement has no effect on black (**ECffP**) or dark-eyed sepias (**E** c^kc^a**ff PB**, **E** c^dc^d**ff PB**, **E** c^dc^a**ff PB**). There is also no effect on brown-eyed browns (**EC ff P bb**, **E** c^dc^d**ff P bb**, etc.). As we have attributed the relatively low intensity of sepia in the c^d combination to a competitive effect of yellow, it must be supposed that the yellow process is affected by **F**, **f** only *after* this competitive action is completed.

The data above suggest that **F**, **f** are specific modifiers of xanthic pigment. This idea is, however, upset by consideration of the combinations with **pp**. In the combinations **EC ff pp B** and **EC ff pp bb**, black and brown are replaced by a pale yellow: **E** c^kc^k**ff pp** and lower compounds of the albino series are pure white. This peculiar relation of **F**, **f** to **P**, **p** can be explained most easily by the hypothesis that **F** can substitute weakly for **P** in its reaction and that there is no other substitute. The fact that **P** is completely dominant

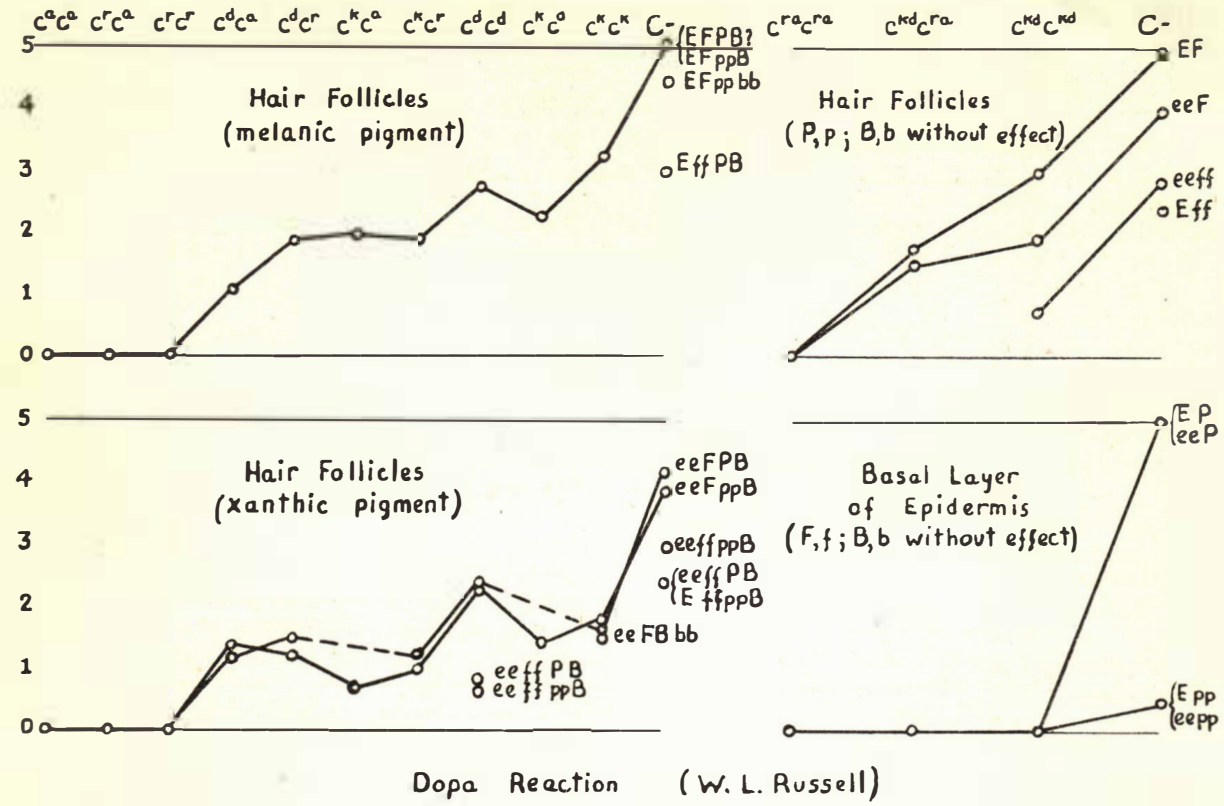


Fig. 5. Grade of dopa reaction in various genotypes from W. L. Russell.

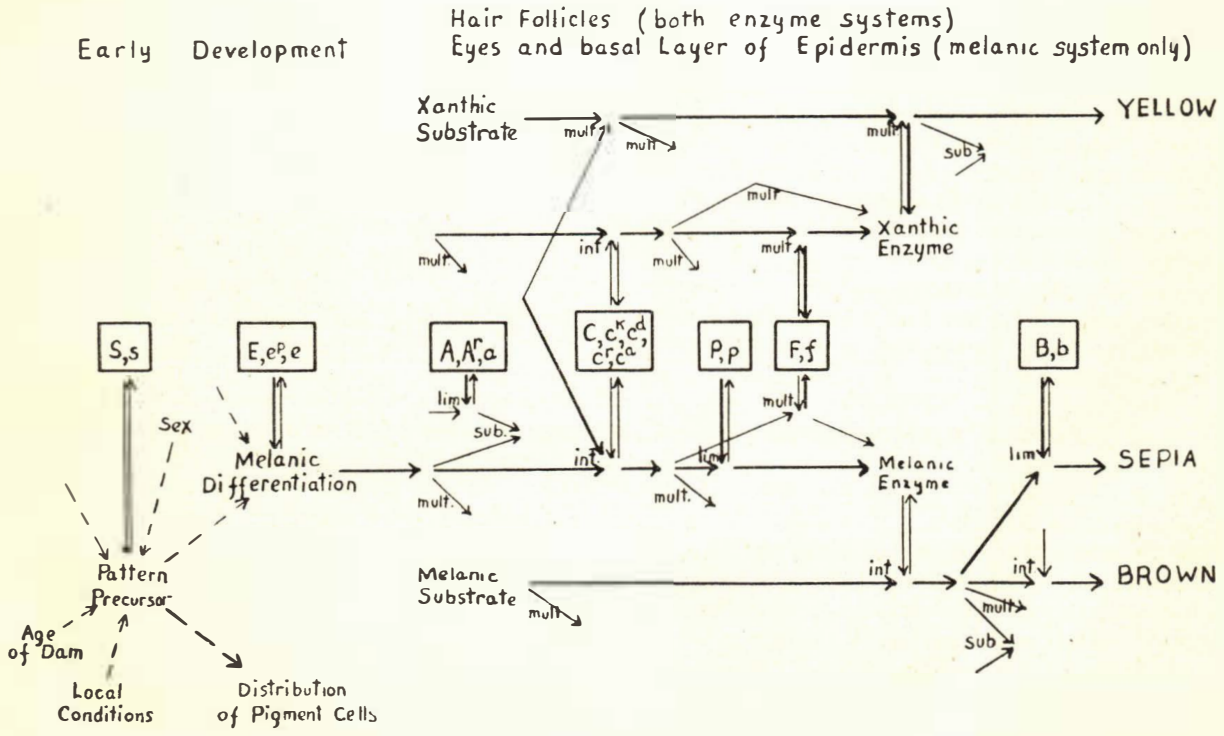


Fig. 6. System of reactions leading to production of yellow, sepia and brown pigment as deduced from gene interactions.

over **p** implies that it is in excess relative to its substrate, transforming all that there is. This explains the absence of any effect on melanic pigment of replacing **F** by **f** where **P** is present. If **P** fails, **F**

The great reduction of the yellow revealed in **E ff pp** (17%) in comparison with **ee ff pp** implies a severe inhibition of yellow by the melanic process at some stage *before* the action of **P** and **F**, but *later*

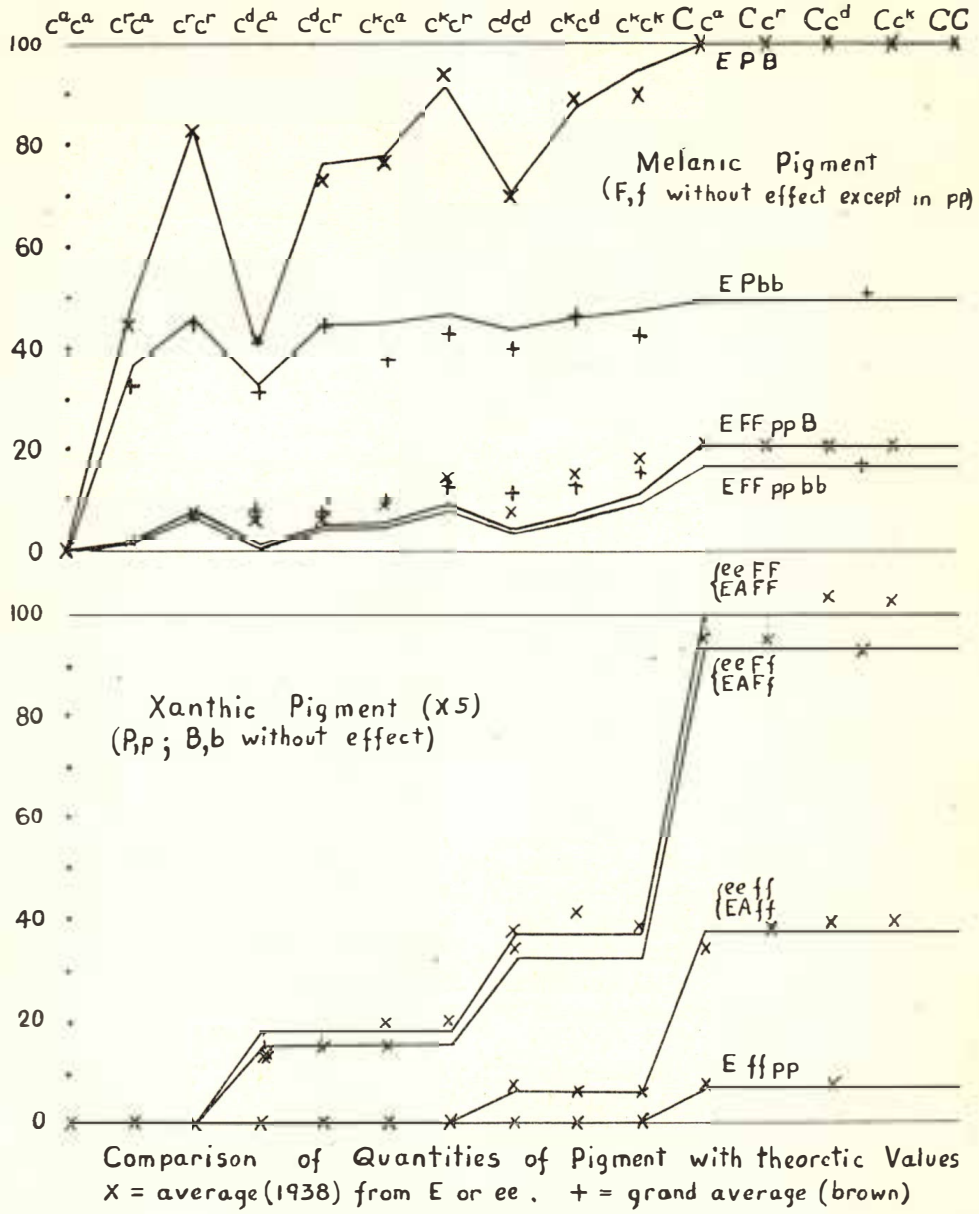


Fig. 7. Average quantities of melanic pigment (above) and xanthic pigment below, compared with theoretical values obtained by substituting appropriate numbers in the system of Fig. 6. Averages based on data for period 1933–8, except in case of brown where grand averages for this and earlier data are used.

carries on the melanic process but at only about 5% of its normal rate. It must be supposed to be approximately multiplicative in effect. Its imperfect dominance (**E Ffpp** being lighter and yellower than **E FF pp**) is in harmony.

than the agouti reaction. This is also indicated by the small amount of yellow associated with melanic pigment in blacks **E C F P B** and pale sepias **E C F pp B**. The latter often fade almost to white, when adult, without revealing any appreciable yellow coloration.

On the other hand, as noted, combinations of c^dc^d, c^dc^r and c^dc^a with **E F pp** (especially **E Ff pp**) are markedly yellowish in appearance. This seems to imply that the competitive effect of sepia on yellow is less in these cases, which means that it occurs either at the same time or later than the melanic **C** reaction. Thus the **P** and **F** reactions must follow the **C** reaction if this reasoning holds.

The dopa reaction

Two very important additional indicators of the activities of these genes are furnished by Dr W. L. Russell's studies of the dopa reaction. His results can apparently be interpreted on the hypothesis that the dopa reaction of hair follicles (affected by the **C** series and by **F**, **f** but not by **P**, **p** or **B**, **b** irrespective of the actual colour of the animal) is an indicator of a xanthic enzyme, while the dopa reaction of the basal layer of the epidermis (strong only in **CP**, weak or absent in **C pp**, absent in c^kc^k **P**, etc., unaffected by **F**, **f**; **B**, **b**) is a weak indicator of a melanic enzyme (Fig. 5). It is postulated that **B** acts on either the substrate or product of action of the melanic enzyme but not on the enzyme itself. Finally, since replacement of **e** by **E** slightly increases rather than decreases the strength of the dopa reaction in the hair follicle, it must be supposed that the inhibitory action of the melanic process on yellow occurs on the substrate or product of action of the xanthic enzyme but not on the enzyme itself (of which the dopa reaction is assumed to be an indicator).

There are diverse effects of temperature which indicate that in some cases the positive reactions are increased by higher temperatures (e.g. ee **ff**), while in othes cases inhibitory reactions are increased (e.g. **E** c^rc^a **PB**, **E** c^ac^a **PB**, **E** c^ac^a **P bb**, etc.), in some cases there seems to be little or no effect (e.g. **eeFF**), while in other cases there seems to be a conflict of opposing tendencies (e.g. **EF ppB**). It does not appear practicable at present to attempt to locate these effects more precisely.

Interpretation

The simplest interpretation of the sequence and nature of the reactions (multiplicative, intermediate, limiting, subtractive) to which we are led by the foregoing considerations is represented in Fig. 6. The consistency of the scheme has been tested by assigning numbers to the reaction constants throughout. The extent of agreement is indicated in Fig. 7 and is undoubtedly capable of some improvement.

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Wrinch, Dorothy M. ***The Fabric Structure of Proteins, with Special Reference to the Problems of Cytogenetics***

There can no longer be any doubt that large numbers of proteins, notably the crystalline globular proteins, have molecular status, and also, like other substances which are chemically less formidable, perfectly definite structures. Yet their molecular weights are large. To account for the existence of these megamolecules it has been suggested that the essential entity in such structures is a peptide fabric (Wrinch, 1936, 1938), which folded round can form closed surfaces having in their skeletons only certain definite numbers of amino acid residues (Wrinch, 1937). Such a type of polyhedral structure is in accord with the known chemical composition of proteins. It explains the existence of definite molecular weights and of special "favoured" molecular weights. Further it suggests that the larger protein molecules may be but aggregations of smaller units, thereby throwing light on the property of reversible dissociation into aliquot parts, found to be characteristic of many proteins. Finally, it provides a picture in terms of which the striking specificity of many proteins such as the enzymes, the virus proteins and the proteins of immunology can be interpreted. This picture of the structure of the crystalline globular proteins, as depending essentially on a peptide fabric, was proposed because the classical view that they are polypeptide chains fails to account for and is indeed in conflict with the experimental facts (Langmuir, 1939).

The arguments which make it impossible to attribute to such definite chemical personalities as the enzyme and virus proteins the classical polypeptide chain structure have, in my opinion, a still greater

cogency in relation to the genic protein structures. I suggest, therefore, that the genic protein structures are also atomic envelopes. The chromosomes may be fibrous only in the sense that these genic protein units, or aggregations of them, are arranged in linear sequence. On this view the genic protein units, which are customarily supposed to be highly basic, are atomic envelopes which depend for their stability on an appropriate concentration of the nucleic acid molecules which are known to be present. Disturbance of this balance, e.g. by a slight shift of *p*H, would cause the breakdown of the closed envelope into an open fabric, thereby providing a protein template which catalyses the formation of a new protein fabric, geometrically capable of forming a new closed envelope, provided the correct complement of nucleic acid molecules is available. The theory that genuine denaturation involves the opening of closed atomic envelopes thus explains how a template becomes available when the acid-base equilibrium is disturbed, and the special geometry of the template shows how the new protein fabric in turn is geometrically capable of forming a closed atomic envelope (Wrinch, 1938).

The essential questions for cytogenetics, namely, the definite chemical personalities of the genic units, and their capacity to duplicate, are thus related intimately to, and in fact are part of the general protein problem. In view of these facts, it seems important that the closest possible contact should be maintained between the two disciplines.

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328

YATES, F. *Statistical Aspects of Animal Experimentation*

The advances in statistical technique to which the needs of agriculturalists experimenting with field crops have given rise are of value in many other fields of research, and particularly to animal experimentalists, who are confronted with very similar problems. Like the plant breeder, the animal breeder is confronted with two distinct problems, namely, the choice of the methods of crossing which will produce the most rapid improvement and fixation of the various characters in which he is interested, and the assessment of the relative genetic value of the different strains or individual animals.

The latter problem is essentially one of experimental design, and it is here that the new technique of agricultural field experiments has most to offer to the animal breeder. In particular, the principle of factorial design enables the relation between breed and environmental conditions to be studied and the most effective balance between them to be determined.

Many variants of the factorial method are possible, the choice of which must depend both on the nature of the problem and the properties of the animal.

The development of field experiments has also served to emphasize the paramount importance of randomization and replication. In genetic problems in which the variability of different strains is of interest, the use of random selection also enables this variability to be properly assessed.

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YATES, F. *Modern Experimental Design and its Function in Plant Selection*

Plant-breeding trials differ from most other types of agronomic experiment in the large number of varieties or lines that have to be compared. As a result Latin squares are impossible for the more extensive trials, and randomized blocks begin to lose their efficiency owing to the large number of plots per block. In the past attempts have been made to overcome this difficulty by the use of controls. It has now been shown, however, that except when the available amount of seed of the new varieties is a limiting factor, the use of controls is unlikely to be as efficient as ordinary randomized blocks, owing to the large amount of ground that must be devoted to the control varieties.

Recently incomplete block and quasi-factorial arrangements have been introduced. These provide an alternative type of design which enables fertility differences to be much more fully eliminated. They can never be appreciably less efficient than ordinary randomized blocks, and generally result in considerable gains in efficiency.

There are several variants of this type of design, most of which can be included under the following heads:

(1) Quasi-factorial arrangements.
(2) Balanced arrangements in incomplete blocks.
(3) Lattice squares.

Quasi-factorial and incomplete block designs possess the common feature that the area under experiment is divided into blocks each of which contains only a few of the varieties. The arrangement is so made that it is possible to eliminate completely the yield differences resulting from differences between blocks. In the case of lattice squares each replication

is arranged in a square, and differences between rows and columns of each square can be eliminated.

Such elimination is equivalent to rejecting entirely the information provided by the comparisons between plots falling in different blocks (or rows or columns of a lattice square). Actually some information is provided by these comparisons, and in extensive experiments it is possible to assess the relative accuracy of the inter- and intra-block comparisons and combine the estimates derived from them by appropriate weighting. If the inter- and intra-block comparisons turn out to be of equal accuracy, such a process is equivalent to analysing the results as if they were derived from an ordinary randomized trial. Even if they are not of equal accuracy this method of analysis will still provide a valid estimate of error of the ordinary varietal means, though these means will no longer provide the most accurate estimates of the varietal differences.

An important development in quasi-factorial and incomplete block designs, which has at present been little investigated, is the introduction of subsidiary treatments such as fertilizers, seeding rates, etc., which can be applied to the separate blocks. In plant selection work such variation in environment is of the utmost importance if a proper relation between environment and genetic type is to be evolved.

It is sometimes thought that the modern designs involving a large number of small plots will not provide material for the quality tests which are so important in most plant selection work. It should be emphasized that the bulking of all the plots of a single variety for quality tests must give as good or better results as a single plot of an equivalent area sown under that variety.

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ZARAPKIN, S.R. *The Measurement of Divergency*

In order to distinguish between differences caused by genotypical and modificatory agencies a statistical method was employed. Divergency means the disproportion in the development of characters in different individuals of the same group with respect to systematical units.

The degree of divergency between two individuals referred to different categories was determined by the comparison of large numbers of characters which were treated by the γ-method (Zarapkin, 1937). The difference of the two categories is based on taking one of them as standard. The differences in the medias of both groups are expressed in σ and the differences between two individuals in percentage from the standard. Thus the influence of the absolute value of the character is eliminated. If we transfer all these σ or all the percentages on the abscissae and the number of the characters of equal deviation on the ordinate we get a frequency diagram of the differences of characters. The media (M) and the standard deviation (here called γ) are calculated as known. M (i.e. the mean deviation of all characters from the standard) depends on the body size and as non-typical was eliminated from the valuation of divergency. The coefficient of divergency is represented by γ. γ means the amplitude of the differences of the characters involved.

Four investigations were performed in this manner:

(1) Analysis of pure modifical divergency in monozygotic twins, and in right and left human body side.

(2) The divergency of the characters of one individual from the M of its population, of other populations and of different subspecies.

(3) Analysis of divergencies between small systematic categories.

(4) Analysis of divergency between related species and genera.

From each analysis we get a gradation of divergency, which was combined to a scale of divergency.

Result of the first analysis: (1) In the case of monozygotic twins and between right and left body side γ varies from ± 3 to $\pm 5\%$. Between both categories there is no real statistical difference. Thus monozygotic twins vary in the same degree as the right and left body side. Therefore the analysis of monozygotic twins may be replaced by the analysis of the body sides. (2) The amplitude of γ in dizygotic twins as well as in brothers and sisters reaches from ± 5 to $\pm 8\%$. Between both values of γ (compare with the above amplitude) there is no transgression. Thus there is the possibility of determining the degree of genotypical identity or genotypical divergency. (3) Between individuals of the same population γ varies from ± 6 to $\pm 12\%$.

The second investigation refers to several populations and subspecies of *Epilachna chrysomelina* (Zarapkin, 1937). The following results were obtained: (1) The γ of each individual of the same population does not exceed $\pm 1\sigma$ in respect to the medias of the whole population. (2) The γ of each individual of another population exceeds $\pm 1\sigma$. (3) The γ of each individual of another subspecies reaches $\pm 2\sigma$. (4) Thus on the basis of quantitatively varying characters it is possible to determine the relation of a single individual to one of the above-named categories.

Investigations on populations of *Epilachna chrysomelina* acquainted us with a third scale of divergency,

which expresses the degree of similarity between small systematic categories.

Finally the analysis of the species and genera of Felinae represents a fourth scale of divergency.

In all cases the increase in the coefficient of divergency is correlated with the decrease of systematic relation.

The main result of our research is, that the divergency, i.e. the basis of evolution, may be measured and expressed by a simple coefficient. This coefficient may be accepted as unit of measurement.

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331

ZIMMERMANN, K. *Some Results of Genetical Analysis in Populations of Wild Rodents*

The existence of widespread heterozygosis in wild populations is now well established in many species. Here are given some examples of this phenomenon in mice and voles.

(1) *Mus. m. musculus* from Berlin-Buch. About 70% of the population is homozygous for the spotting gene s. The manifestation varies from a few white hairs on the belly to one or two central spots and sometimes a white tail-tip. Inbreeding and selection for fifteen generations has demonstrated that plus-modifiers extending the manifestation to the dorsal parts are completely absent in this stock. One of the wild individuals from Berlin-Buch was heterozygous for a new mutation "hydrocephalus$_2$", genetically different from the "hydrocephalus$_1$" found by Clark in an American Laboratory stock.

(2) *Mus. m. musculus* from a village near Bremerhaven. A dominant factor producing a darker agouti colour (almost black when homozygous) is present in over 70% in the population. One of the few specimens bred was heterozygous for the mutation "dwarf", identical with the American dwarf (Snell, 1929).

(3) *Mus. m. musculus* from Spiekeroog (Frisian Island). A single specimen was killed, apparently containing the factor c^h (Himalayan) of the albino series. This factor, known in the rabbit, guinea-pig and cat, had not been detected previously in the house-mouse. Attempts are being made to get this mutation from the Spiekeroog population.

(4) *Apodemus a. agrarius.* In the almost isolated population of the Berlin Zoological Garden a recessive gene frequently occurs which is probably homologous to the "pink eye" of the house-mouse.

(5) *Clethrionomys glareolus*, red-backed vole. Among 300 animals from Berlin-Buch with the usual red dorsal area a single male was caught with a brown dorsal area, typical for the alpine subspecies *C. g. nageri.* This difference in colour was found to be caused by one dominant factor. The same male was heterozygous for a new mutation "black and tan". Inbreeding with two Berlin-Buch animals showed (1) a dominant factor with small penetrance, causing "open fontanelles" in adult skulls, (2) one or several (not yet analysed) lethal factors. The very young mice are externally normally developed, but either stillborn or dying within the first days. A female red-backed vole, caught in eastern Prussia, was heterozygous for a recessive "Chorea" mutation, probably homologous to the shaker in the house-mouse and *Peromyscus.*

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